A PHYTOGEOGRAPHICAL ANALYSIS OF *TAXUS* (TAXACEAE) BASED ON LEAF ANATOMICAL CHARACTERS

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ABSTRACT

A phytogeographic analysis of 845 *Taxus* specimens is presented based on leaf anatomical characters for the number of stomata rows in a stomata band and the number of epidermal cells that lack papillae between the leaf margin and stomata band. The specimens are arranged by continent, country, state or province, and species, and represented geographically on three maps: (1) North America, (2) the Euro-Mediterranean, and (3) Asia. *Taxus* is least diverse and most distinct taxonomically in North America, and most diverse and least distinct taxonomically in southwest China. Stomata data show several clines in North America, an obvious south to north decrease for the Mesoamerican yew (*T. globosa*) and Pacific NW yew (*T. brevifolia*) populations combined, and a less obvious reverse cline for the Canada yew (*T. canadensis*). The results are discussed in review of other paleobotanical data. It is suggested that *Taxus* immigrated to North America from Asia across a Pacific land connection during the Cretaceous, and from Europe to North America across North Atlantic land bridges during the Tertiary. The low diversity of *Taxus* in North America is suggested to be the result of the K/T extinction event. In the Euro-Mediterranean, evolution of *Taxus* is suggested to have been impacted more by extinction as a result of climatic changes during the Tertiary, and by hybridization during the Pleistocene. The greater diversity in SW China is indicated to be the result of less extinction there and more frequent hybridization during the Pleistocene, not only among authochtonous species, but also allochtonous species as a result of the Himalayan uplift.

CHINESE ABSTRACT

基于每一条气孔带内气孔列数目以及叶边缘和气孔带之间缺乏乳突的表皮细胞数目的解剖特征，本文对 845 份红豆杉属 *Taxus* 标本进行了植物地理分析。标本按洲、国家、州或省以及种来排列，其地理分布显示在 3 幅地图上：（1）北美，（2）欧洲—地中海，（3）亚洲。红豆杉属在北美的多样性最低且分类上区别最明显，而在中国西南部的多样性最高且分类上区别最不明显。气孔数据显示红豆杉属在北美有几个渐变群，中美洲红豆杉 *T. globosa* 和太平洋西北红豆杉 *T. brevifolia* 的居群由南向北明显减少，加拿大红豆杉 *T. canadensis* 由北向南减少得不太明显。综合考虑了古植物学资料，这些结果支持以下一些假说。红豆杉属在白垩纪和第三纪分别从亚洲和欧洲穿过太平洋陆地连接和北大西洋陆桥迁移到北美。白垩纪—第三纪界线绝灭事件造成了红豆杉属在北美低的多样性。第三纪气候变化造成的绝灭和更新世发生的杂交对欧洲—地中海地区红豆杉属的演化影响更大。由于喜马拉雅山的抬升，红豆杉属的土著种和外来种在更新世的杂交比较频繁，而且在中国西南部绝灭较少，所以该属在中国西南部的多样性较高。

INTRODUCTION

The genus *Taxus* has included eight geographically defined species: (1) *T. baccata* L.—Europe, N Africa and SW Asia (Franco 1964), (2) *T. cuspidata* Siebold & Zucc.—temperate E Asia (Krüssmann 1985; Ohwi 1965), (3) *T. wallichiana* Zucc.—Himalayas (Krüssmann 1985), (4) *T. sumatrana* (Miq.) de Laub.—S China, Philippines, Taiwan, Sulawesi, and Sumatera (de Laubenfels 1988), (5) *T. globosa* Schltdl.—N Central America to Mexico (Ferguson 1978), (6) *T. brevifolia* Nutt.—NW North America (Ferguson 1978; Hils 1993), (7) *T. floridana* Nutt. ex Chapm.—W Florida (Ferguson 1978; Hils 1993; Price 1990), and (8) *T. canadensis* Marshall—NE North America (Ferguson 1978; Hils 1993; Price 1990). Except for *T. sumatrana*, these were also recognized by Pilger (1903, 1916, 1926) as subspecies of *T. baccata*.

These eight geographically defined taxa—generally accepted as species (Bailey 1933; Farjon 1998; Hils 1993; Krüssmann 1985; Rehder 1940; Silba 1984)—have not been clearly distinguished (Ferguson 1978; Price 1990), including several other species and varieties that have been recently recognized (Farjon 1998, 2001; Fu et al. 1999); however, I will show that this traditional geographical classification is distorted to recognizing more species where diversity in the genus is least (North America) and less species where

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diversity is greatest (SW China). This will be based on quantitative leaf character attributes for the number of stomata rows (SR) in a stomata band, and the number of marginal cells (MC) across an abaxial marginal zone without papillae. These data will be summarized on geographical maps of North America, Euro-Mediterranean, and Asia, and analyzed in the results section of this study. This is followed by a discussion of phytogeographical relationships. Data for all herbarium specimens studied are provided in an appendix according to continental and political regions and taxonomy.

MATERIALS, STANDARDS AND METHODS

MATERIALS.—The materials of *Taxus* include 845 specimens of fresh and dried branchlets with leaves from throughout the natural range of the genus (Appendix), and an undetermined number of specimens from cultivated plants in Australia (1), England (~50), France (~20), and the United States (~300), and from miscellaneous other sources, the main one was Phyton, Inc (~65), now Phyton Biotech, a commercial company specializing in producing taxol from tissue culture of *Taxus*.

STANDARDS.—The genus *Taxus* Linnaeus (Taxaceae Gray) is defined by cone and leaf morphology (Florin 1931, 1948c, 1951) in relationship to other "taxad" genera, characterized by producing an arillocarpium (Spjut 1994)—a type of cone in which the seed is subtended by a fleshy arillate bract (Airy Shaw 1973; Cheng & Fu 1978; Florin 1948a; de Laubenfels 1988).

Taxads include both extant and extinct taxa; the extant genera, in addition to *Taxus*, are *Amentotaxus* (5–6 spp., China, Vietnam), *Torreya* (6 spp., E Asia, N America), *Austrotaxus* (1 sp., New Caledonia), *Cephalotaxus* (8–11 spp., E Asia), and *Pseudotaxus* (1-2 sp., China) (Fu et al. 1999). Molecular studies employing ribosomal RNA (Chaw et al. 1993, 1995), chloroplast DNA (Tsumura et al. 1995), or RAPD (T. Wang et al. 2000), suggested *Amentotaxus* and *Torreya* to be more closely related to each other than to *Cephalotaxus* or *Taxus*, and that *Cephalotaxus* is basal to two clades, (1) *Torreya/Amentotaxus* and (2) *Taxus/Pseudotaxus/Austrotaxus* (Cheng et al. 2000); however, whether these clades should be treated in separate orders, families, subfamilies, or tribes, is controversial (Hill 1998).

Cones.—*Pseudotaxus* and *Taxus* produce a terminal seed on a lateral (secondary) short shoot (André 1956; Dupler 1920; Miller 1988) that is only partly surrounded by a loose cupular bract, whereas in other genera the seed is more fully and tightly covered by the aril (Florin 1948b; Sahni 1920). *Cephalotaxus* is distinct for its biovulate cone scales from which usually only one ovule matures (Singh 1961). *Amentotaxus* differs for its terminal, "racemose" male shoots (Cope 1998; Fu et al. 1999). The *Austrotaxus* cone was regarded as isolated from other taxads based on anatomy of the seed coat (Bobrov et al. 2004).

The closely related *Pseudotaxus* (1–2 spp., China, Fu et al. 1999) differs from *Taxus* by a white arillocarpium (Cheng 1934), and additional sterile scales in male cones (Florin 1948c).

Leaves.—*Taxus* leaves are differentiated from those in other taxad genera by **papillose** cells that define the "stomatic apparatus" (Dilcher 1969; Florin 1931, 1948c, 1951, 1958). This apparatus includes 4–8 small subsidiary papillose cells that encircle each stoma (Florin ring) and adjacent (accessory) papillose cells (Figs. 1A, 1B, 1C). Stomata develop in longitudinal rows (periclinal) in a stomatal region divided into two bands by a midrib (e.g., Fig. 1A). The midrib and marginal cells vary in size, shape, and development of papillae. Further details—with photomicrographs—can be found in Ferguson (1978), Florin (1931, 1951), Jinxing and Yuxi (2000), Kvaček (1984), and Kwei and Hu (1974).

Mammillae, not to be confused with papillae (Bertrand 1874), develop singly over most of the cell's surface as large lens like bumps. Under a dissecting scope (30×) they appear most conspicuous along leaf margins, less so on the epidermal surfaces (adaxial or abaxial). Papillae, by contrast, are smaller and numerous on a cell—like pimples. They develop in 1–3 distinct or concrescent rows, generally discernible only under a microscope—at least 100×, and only on the abaxial surface. Papillae are always present in stomata bands, gradually diminishing in prominence outside the bands towards the leaf margins, and may develop entirely or partially or not at all on midrib cells.

The development of stomata in rows and their differentiation by papillose accessory cells, which together make up the stomata band, are the most distinguishing features of *Taxus* relevant to data in this study, compared to other extant genera of taxads (Florin 1931, 1951). For example, *Pseudotaxus* has glaucous stomata bands (Cheng 1934; Florin 1931, 1948b, 1948c, 1948d) devoid of papillae, except on subsidiary cells, and more stomata rows per band—23–28 rows (Florin 1948c), in contrast to 4–21 rows in *Taxus* (Appendix). *Amentotaxus* and *Torreya* (Amentotaxaceae) have papillose glaucous bands largely of subsidiary cells (periclinally arranged), rather than accessory cell types (Florin 1951, 1958). *Austrotaxus* (Austrotaxaceae; Nakai 1938; Florin 1958), which also differs conspicuously by its long-linear leaves—comparable to some *Podocarpus* spp.—has stomata evenly scattered across the entire abaxial surface without clear differentiation of rows and bands in which the epidermal cells are similar to those on the adaxial surface—irregularly quadrate (or pentagonal) as in *Taxus*. These differences, and the presence of other features such as sclereids and resin canals in leaves of *Torreya* (Bertrand 1874) and *Cephalotaxus*, would seem to support classification of the taxads in different families (Amentotaxaceae, Austrotaxaceae, Cephalotaxaceae, Taxaceae).

The features of the stomata band that distinguish *Taxus* from other extant taxads do not apply to extinct taxads, however (Florin 1951, 1958; Harris 1976a, 1976b; Kvaček 1984; Miller 1977). Photomicrographs of many taxad fossils from Jurassic deposits presented by Florin (1958) show remarkable detail that are strikingly similar to extant *Taxus* in leaf epidermis (Kvaček 1984; Meyen 1984), except for narrower stomata bands with fewer stomata rows (Kvaček 1984). Indeed, some leaves, which included twigs and arillocarpia, were assigned to *Taxus*; these are *T. bornholmiensis* Florin with 4–5 stomata rows, *T. harrisii* Florin with 5 stomata rows, and *T. jurassica* Florin with 3–5 stomata rows; however, none of these appear to belong to the genus *Taxus*. Harris (1976a, 1976b), for example, transferred *T. jurassica* to *Marskea*, an extinct genus characterized by opposite-decussate leaves (Florin 1958; Harris 1976b), which are clearly evident in Florin's (1958) photograph of *Marskea jurassica*. Jurassic taxads include many other extinct genera (Florin 1958) that may have existed since the Triassic (Florin 1951; Meyen 1984).

Epidermal cells adjacent to leaf stomata bands, the midrib and marginal areas, are usually papillose in part. Epidermal cells on the abaxial surface nearest the leaf margin appear to have evolved in some species by extension (folding) of the upper (adaxial) surface to the lower (abaxial) surface; leaves of many specimens are revolute along their margins in which the abaxial epidermal cells are often more similar to those above than to the adjacent cells below (Nicolosi 1982).

The comparative morphological relationships of *Taxus* to other extant taxads (Florin 1931, 1948c; Appendix) indicate that the ancestral *Taxus* leaf had a partially differentiated abaxial epidermis in which stomata developed in definite rows but not in distinct bands. Evidence for this can be seen in *T. wallichiana* and allied species in the E Himalayas and SW China. Their leaf stomata occur not only in stomata bands, but also on the abaxial midrib; essentially, stomata develop across the entire abaxial leaf surface to within several cells of the margin—in up to 21 rows. The abaxial marginal and accessory epidermal cells are all nearly rectangular and papillose—in sharp contrast to the epidermal cells on the adaxial surface that are much shorter, ±trapezoidal-pentagonal, and without papillae.

METHODS

More than 1,000 herbarium specimens (A, BH, BM, BOLO, E, GH, K, M, NA, NY, P, PE, PH, S, U, US; Holmgren et al. 1990) were studied of *Taxus* throughout the natural range of the genus to assess morphological variation in characters that involve branches, bud-scales, leaves, and cones; 845 are cited in the appendix, and additional specimens are mentioned in this paper. Each specimen was photographed with a Nikon camera using 35 mm color film with 35 mm and 60 mm lenses. Stafleu and Cowan (1976–1988) were consulted for location of types, other specimens of historical relevance to this study, and references.

From each herbarium specimen of *Taxus,* one mature leaf was selected for microscopic study of anatomical features. The *Taxus* leaf was soaked in water for 8–16 hrs. The leaf was then transversely sectioned in the mid region as bryologists routinely section leaves of mosses for taxonomic identifications. With a single-edge razor blade and dissecting needle as a guide, 5–10 transverse sections were generally made. Then an abaxial epidermal layer was removed from both remaining leaf portions, generally 0.5–2.0 mm in length, by scraping mesophyll parenchyma from the epidermal layer with a razor blade. Occasionally, the entire abaxial leaf

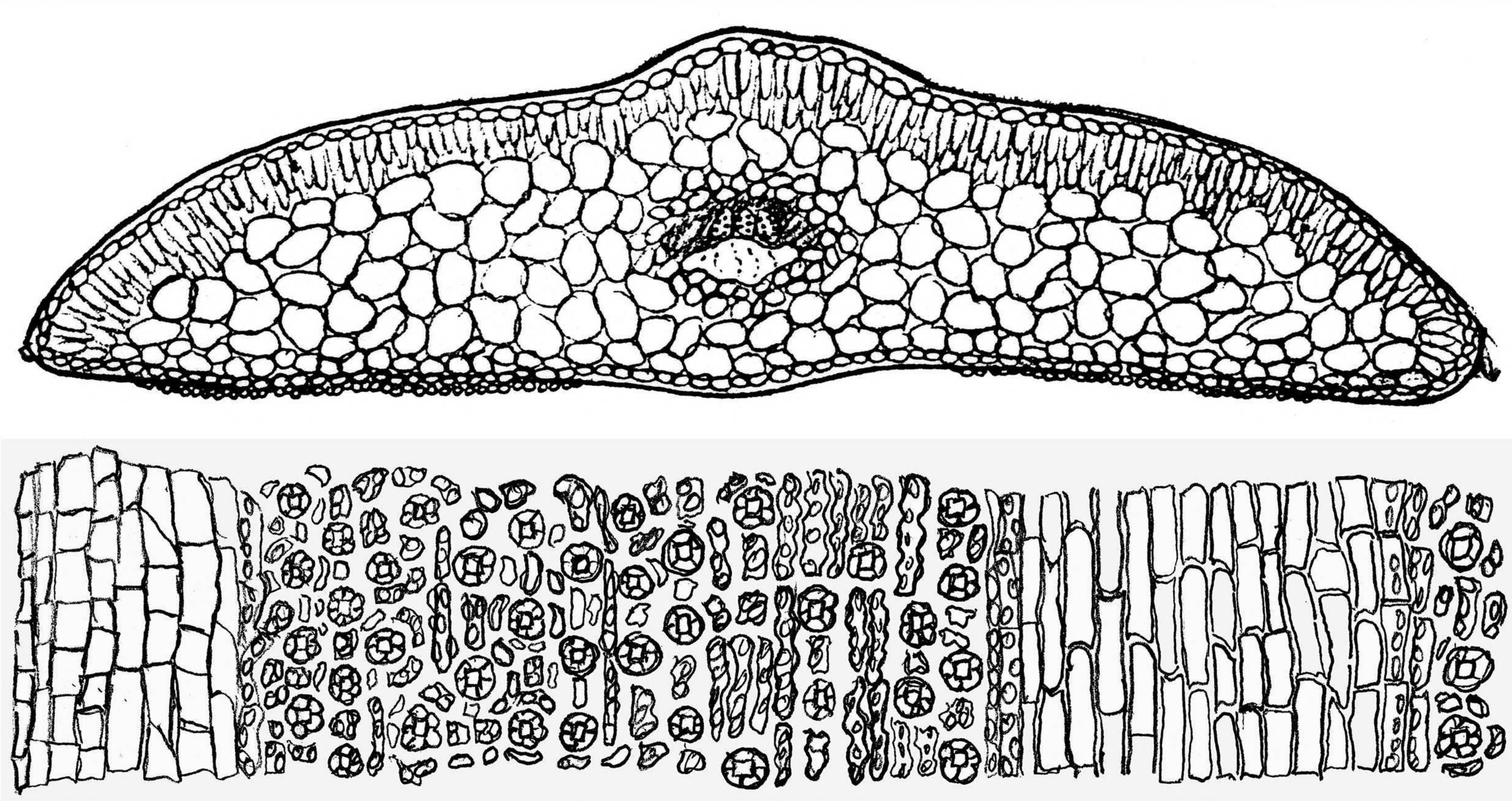


Fig. 1A. Mid leaf sections of *Taxus caespitosa* var. *latifolia*, from a cultivated plant in Maryland, U.S.A, *Spjut 10485* (wba), representative of the *Baccata* Group, *Cuspidata* Alliance. **Top:** transverse section (T-sect.), ~100×, showing elliptical shaped epidermal cells, mesophyll layers of anticlinal palisade layer of parenchyma and spherical parenchyma cells, drawn by Karen Parker. **Bottom:** abaxial epidermal layer from margin (left) to midrib (right), ~250×, showing a marginal border of 8 smooth (non-papillose) cells wide followed by a stomata band with 13 rows of stomata, and a midrib of mostly smooth cells, drawn by R. Spjut.

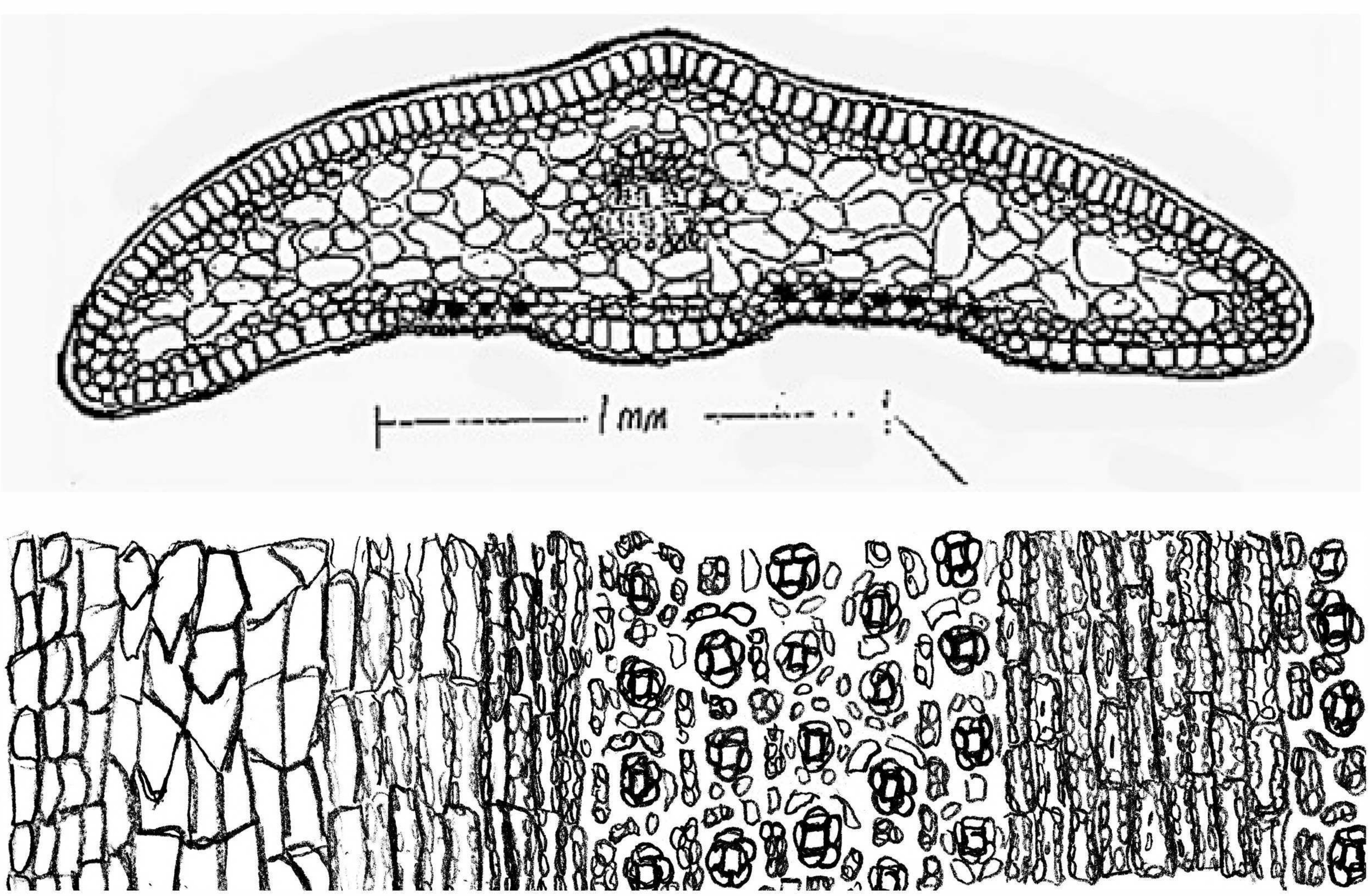


Fig. 1B. Mid leaf sections of *Taxus brevifolia* var. *reptaneta* from Siskiyou Co., California, U.S.A., representative of the *Wallichiana* Group, *R. Spjut & T. Spjut 11835* (wba, type). **Top:** T-sect. ~ 100× shows tall angular epidermal cells, drawn by Karen Parker. **Bottom:** abaxial epidermal layer from margin (left) to midrib (right), ~250×, shows marginal region of 10 smooth cells across of which 6 rows are inflated, followed by 8 rows of papillose cells, 5 stomata rows, and a papillose midrib, drawn by R. Spjut.

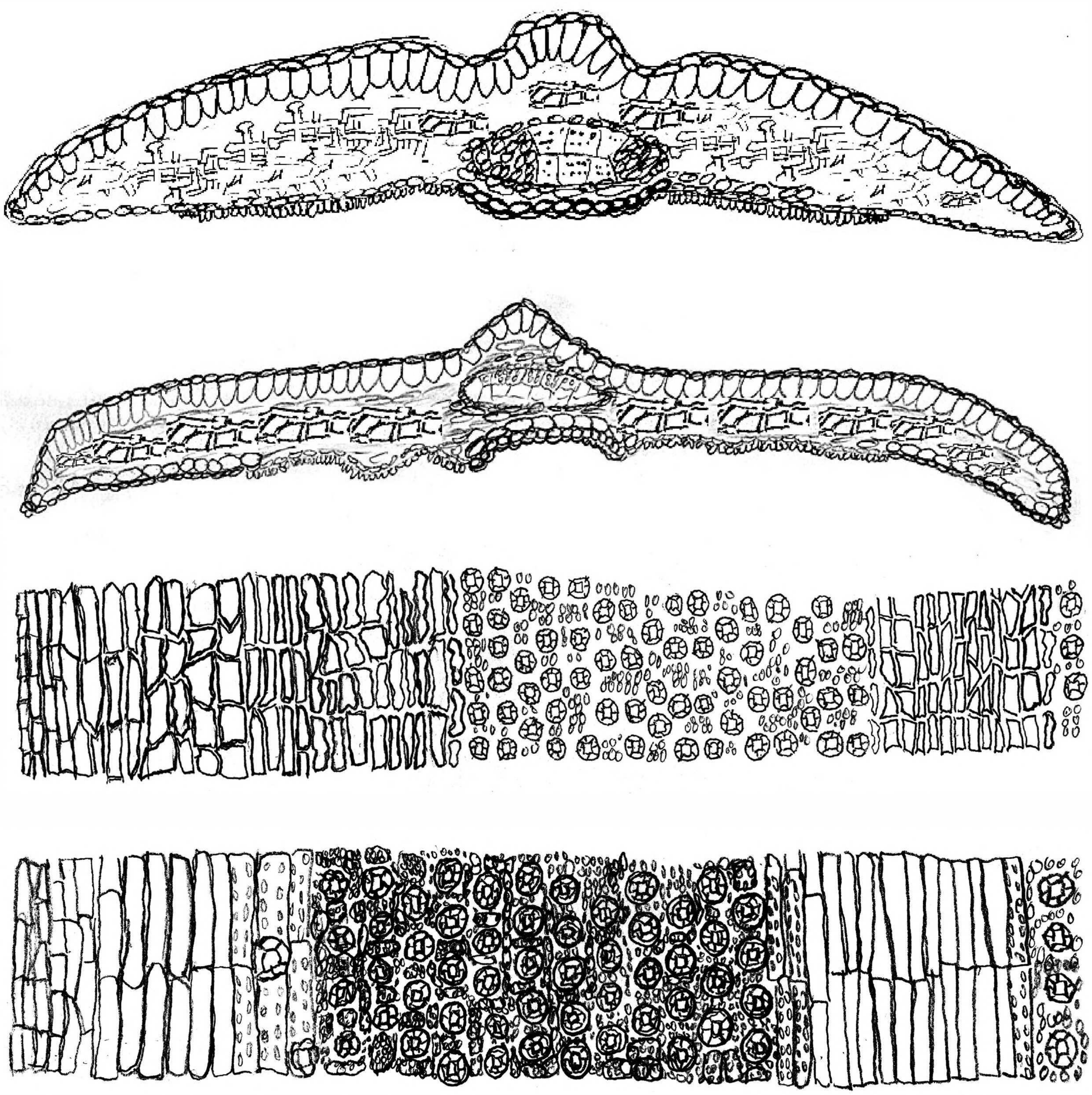


Fig. 1C. Mid leaf sections representative of the *Taxus Sumatrana* Group, drawn by R. Spjut. From top to bottom: Top: *T. mairei* var. *mairei* from Guangdong (China), *Tsang 20694* (US), showing elevated and truncated midrib along abaxial surface with enlarged epidermal cells in comparison to smaller elliptical epidermal cells on adaxial surface, the lower T-section, *T. mairei* var. *mairei* from Yunnan, *Maire s.n.*, isotype, showing truncated and channeled midrib with larger spherical parenchyma cells lying against smaller epidermal cells—most conspicuous along midrib and marginal zones. Lower two sections: abaxial epidermis from margin to across the midrib; upper most from Guizhou, isotype (A) of *T. speciosa*, showing marginal region of 23 smooth cells in width, a stomata band with 16 rows of stomata, and a smooth midrib; the lowest section from holotype of *T. sumatrana*, showing long rectangular cells and 12–14 stomata rows.

surface and a medial portion of the adaxial epidermis were removed. All sections were examined under magnifications of 100×, 250×, and 400× (Nikon binocular microscope) for cell shape, number of stomata rows, number of cells marginal to stomata bands, and for papillae position and distribution across the abaxial leaf surface. The results were sketched and described on small packets 3 × 5 inches. A temporary slide of the sections and photographs of the herbarium specimen were retained for each packet. Leaves from fresh specimens were also similarly studied throughout the range.

Figs. 1A–1C show diagrammatic leaf sections of the mid region that is representative of three species

Fig. 2A. Number of stomata rows per band (SR) in leaves of *Taxus* plotted from locality data on representative herbarium specimens from North America; see Appendix for specimen data. Specimens from northern Mexico indicated in yellow numbers are not easily distinguished from those in Florida; therefore, these are considered *T. globosa* var. *floridana*.

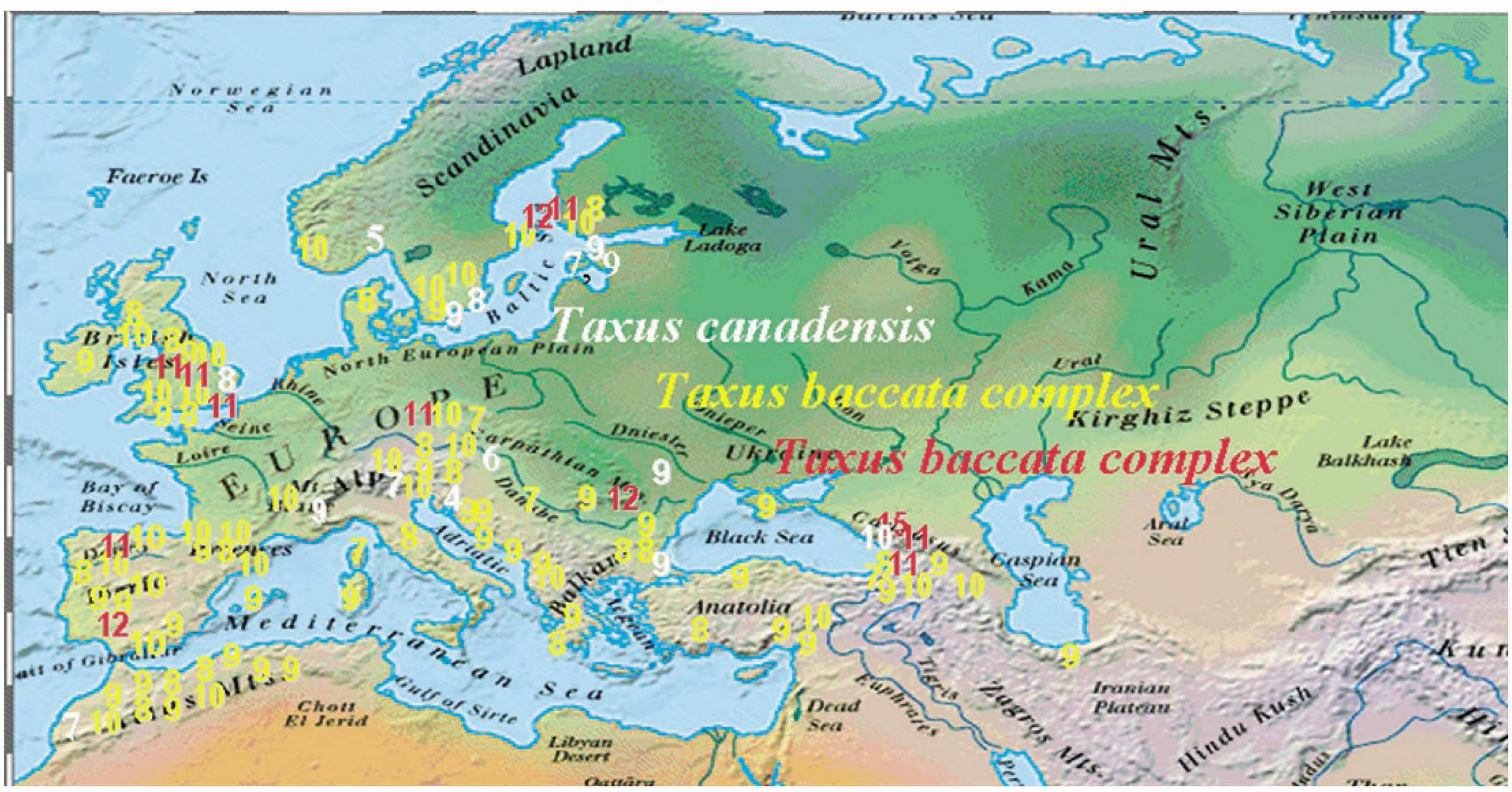


Fig. 2B. Number of stomata rows per band (SR) in leaves of *Taxus* plotted from locality data on representative specimens from the Euro-Mediterranean; see Appendix for specimen data. Most specimens were found to have 8–10 stomata rows per band as indicated in yellow numbers. Occasional plants with higher counts, 11–15 stomata rows per band, are shown in red. Both yellow and red numbers belong to the *Baccata* Alliance. Numbers in white belong to *T. canadensis*. Most *T. canadensis* have less than 8 stomata rows per band, but a few with higher counts—up to 10 stomata rows per band—are shown.

groups of *Taxus*. These include (1) a complete transverse section and (2) an epidermal portion of the abaxial surface from one margin to across the midrib. As previously indicated, similar sketches were made on 3.5 × 5 inch (8 × 12.5 cm) packets for most herbarium specimens studied except only portions of the stomata and marginal areas were drawn, while number of stomata in a band and number of marginal cells adjacent

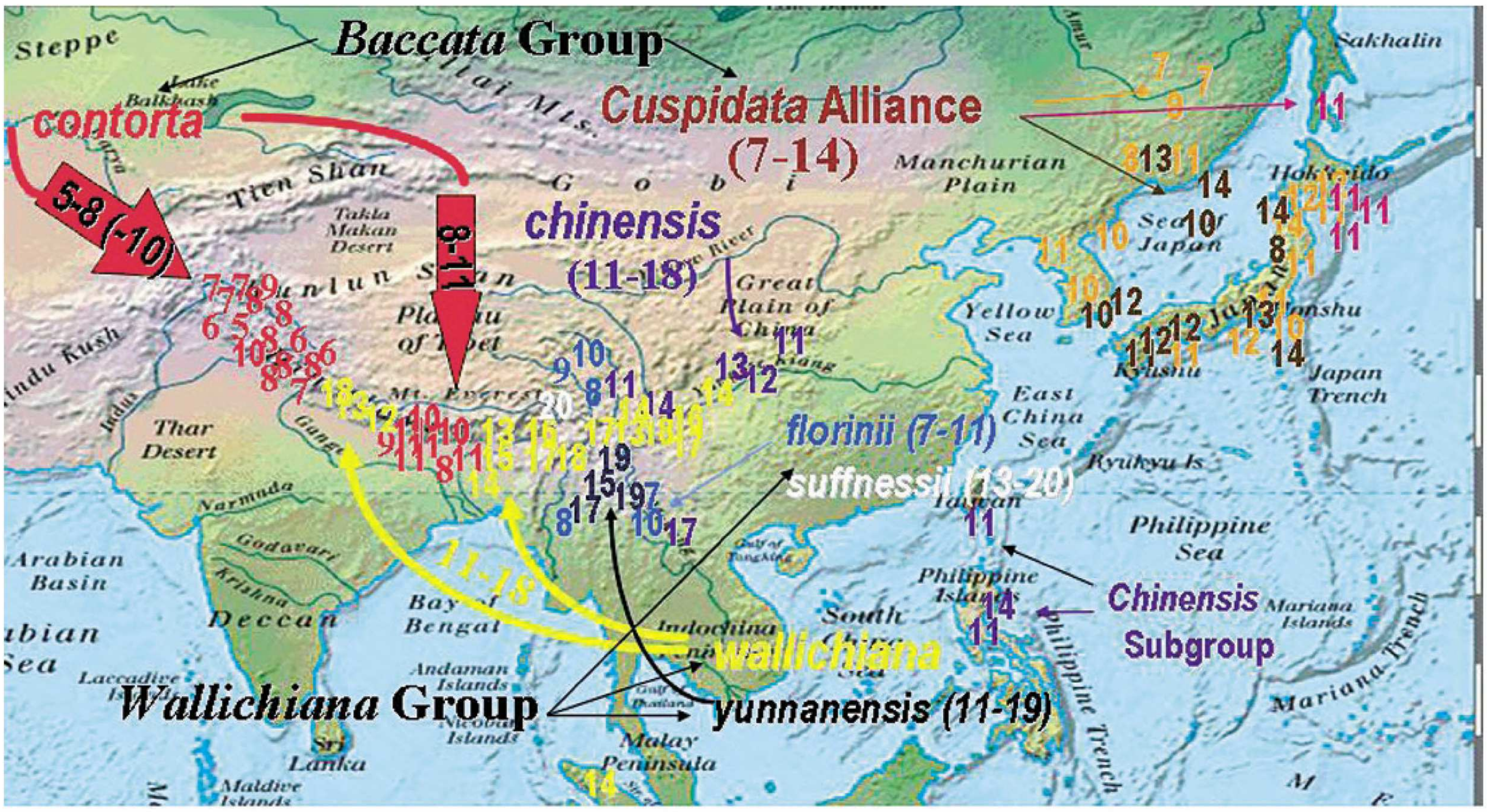


Fig. 2C. Number of stomata rows per band (SR) in leaves of *Taxus* for representative specimens in E Asia of the *Baccata* and *Wallichiana* Groups; see Appendix for specimen data. The *Sumatrana* Group, which is common in SE China, is not shown to contrast the difference between the *Wallichiana* and *Baccata* Groups. The *Wallichiana* Subgroup includes *T. suffnessii* in white, *T. florinii* in blue, and *T. wallichiana* var. *yunnanensis* in black. The *Chinensis* Subgroup within the *Wallichiana* Group includes *T. chinensis* shown in purple in mainland China and related species in the *Chinensis* Subgroup in the Philippines, Sumatera, Sulawesi, and Taiwan, and also two species in mainland China, in yellow. The *Cuspidata* Alliance includes four species; *T. cuspidata*, *T. biternata*, and *T. caespitosa*, in maroon, and *T. umbraculifera*, in black. Note higher counts for *T. contorta* (8–11) and lower counts for *T. wallichiana* (11–14) where the ranges of these taxa overlap in the central Himalayas. The widest range in number of stomata rows was found in N Myanmar to SW China where *T. florinii* is recognized to have 7–12 rows per band, and *T. suffnessii* from 13–20 rows per band.

to stomata bands were recorded. The leaf margin can be difficult to pinpoint when leaves are rounded along margins. This is determined by the smallest cell that is usually mammillose. Both types of leaf sections were examined to determine where papillae develop on cells between the margin and stomata band.

Variation due to mechanical preparation, error in counting, and environmental factors (Deryugina & Nesterovich 1981), were only generally assessed—for practical reasons—from duplicates that were unintentionally included in this study, occasional field collections that were collected at various heights from one or several trees of a population (top, middle, and lower branches of *T. brevifolia* from trees in California and Oregon), and from test cases of selected leaves at various developmental stages from shrubs in cultivation. Practical reasons include damage to herbarium specimens caused by removing a leaf, and the time required to prepare leaf sections and record data, approximately one hour for each specimen.

Herbarium specimens studied are listed in an appendix with data on numbers of stomata rows per band (SR) and numbers of marginal cells (MC) without papillae. Specimen data are arranged by continent, then by country within continents, and finally by taxa, generally from south to north in North America, and from west to east in Eurasia, and then east and south from the Himalayas to Indonesia. Leaf anatomical data are further arranged by decreasing order in number of stomata rows (SR), and by increasing order in number of marginal cells (MC) except for *T. canadensis*, the *Sumatrana* Group, and for duplicate specimens belonging to the same species, or duplicate specimens from the same locality or collection number. Only minimal collection data are cited, although for many specimens data were minimal. If the stomata count varied on each side of the midrib of a single leaf, this is indicated by a slash; for example, *T. canadensis* frequently had 5 stomata rows in one band and 6 in the other (5/6). A dash between numbers indicates a variable range, especially when more than one leaf from the same specimen was studied, or a dash alone indicates absence of data. It should be remembered that these data are a byproduct of an overall taxonomic study of the genus *Taxus* (see Spjut 2007); i.e., they were not compiled with this paper in mind. Additional character features that appeared to correlate with the findings are also noted (e.g., length of epidermal cells/width of epidermal cells or l/w).

RESULTS

Numbers of Stomata Rows (SR).—Figures 2A, 2B and 2C show numbers of stomata rows per band on maps of North America, Europe, and Asia, respectively, for representative specimens listed in the Appendix. Each number represents a count from a single leaf of a herbarium or fresh specimen; the datum is plotted at the general location where it was reported to have been collected. Where the count varied on each side of the leaf midrib, or among duplicate specimens, the highest number was scored.

Stomata data for duplicate specimens, or among specimens from different plants at the same locality, are summarized under five cases as follows:

(1) For 62 duplicates of herbarium specimens included in this study, the same number of stomata rows per band was found in 19 duplicate specimens. Among the remaining 43 duplicates, 17 differed only by 1 row, another 17 differed by 2 rows, 6 varied by 3 rows, and 3 varied by as much as 4 rows. Duplicates that varied by 4 stomata rows appear to have been collected from different habitats within the same general locality. Examples are *Farges 128* from Sichuan, *Tsiang Ying 1425* from Guangdong, and several cases where the same collection number was reported from multiple locations, *Wilson 1265*, from two sites in Sichuan and one in Hubei, and *Wilson 4053* from two locations in Sichuan (Rehder & Wilson in Sargent 1914).

(2) From a single shrub of *T. caespitosa* Nakai var. *latifolia* (Pilg.) Spjut in Maryland, ~35 yrs of age and 3 m in height, 16 leaves were selected from branchlets with various exposures to light and age (1^{st}–2^{nd} yr). With one exception, 15 were found with 13 stomata rows per band; one leaf—plucked from a well-shaded branchlet near the main trunk—had 16 rows.

(3) From trees of *T. brevifolia*, leaves from top, middle, and lower branches had the same count at two sites—one in California, and another in Oregon—but varied by 1–2 rows in leaves from different trees at the same sites.

(4) In Taiwan, individuals of a population collected on five occasions (Appendix) had the same number of stomata rows at one site (Tongshi 7), but varied from 11–14 rows per band at two other sites (Tongshi 5, Tongshi 6).

(5) The age of the leaf was apparently not a factor in 20 leaves studied of one cultivated individual of *T. mairei* (Lemée & Lév.) S.Y. Hu *ex* T.S. Liu var. *speciosa* (Florin) Spjut; 16–18 stomata rows per band were found in all leaves from buds to 3^{rd} yr branchlets.

Generally, the number of stomata rows per band varied by a count of 3 for about half of the individuals or species. In NW North America (*T. brevifolia*), this occurred frequently among different individuals within a population, whereas in Europe (*Baccata* Alliance) leaves of *Taxus* exhibited the same range in variation whether obtained from the same plant or from different plants at the same site. A wider range, 13–18 stomata rows, in the E Himalayas (*T. wallichiana*), and a narrower range, 5–6 or 6–7 stomata rows, in NE North America (*T. canadensis*), were also evident.

Despite this range in variation, the numbers of stomata rows per band in North American *Taxus* (Fig. 2A) show a distinct cline from south to north for the *Wallichiana* Group (Central America to Florida, California). Specimens from Honduras to southern Mexico had 7–11 rows per band (Bertrand 1874); those from N Mexico and Florida had (5–) 7 (–8) rows per band in further contrast to 4–7 (–9) stomata rows per band in the Pacific NW. This northward decline in stomata rows per band is also apparent within the Pacific NW by the highest count of 9 rows found in specimens from California, compared to the lowest count of 4 rows from specimens at more northern locations—in the Rocky Mountains. This cline was also noted to be associated with an increase in length of epidermal cells relative to width (l/w), ranging from an average of ca. 3× l/w to 8× l/w.

A reverse cline, however, is evident in the NE North America by 9 rows per band occasionally found in specimens from Newfoundland, compared to the more common 6 rows per band as reported by Bertrand (1874), which includes specimens from Quebec to Ontario, south to Kentucky (Spjut 1998a, 2000a, 2000b).

In the Euro-Mediterranean, *Taxus* leaves most often had 8–10 stomata rows per band (Fig. 2B); however, notably higher counts and lower counts were found at widely scattered locations (Fig. 2B, red and white numbers; appendix in bold type). Among the higher counts are specimens from the Caucasus Mountains, one with 15 rows (*Princeps Kascelsky, ex. Herb. Hort. Imper. Petro*), another with 13 rows (*Woronowa s.n.*). Occasional specimens with 12 rows are from Bosnia (*Biol. Inst. Dubrovnik 37*), Romania (*Topa, Bot. Mus. Exsic*), Finland (*Florstöm s.n.*), Portugal mainland (*Yoller 61*), Portugal Azores (*Goncalves 4625*), and Algeria (*Swingle s.n.*). Those that were noted to differ in other morphological features are indicated in bold type, including also specimens with 11 stomata rows per band, such as one specimen from England (*Bowden & Hillman 433*) that had globose shaped epidermal cells, instead of the usual elliptical shape; others such as *Hauti 28894* from the British Isles and *Busch s.n.* from the Caucasus Mountains had a broader marginal zone of bare cells, as indicated later under results for marginal cells. A higher number of stomata rows with a wider leaf margin indicate a higher density of stomata as seen in the *Cuspidata* Alliance. The range of variation for the *Baccata* Alliance was greatest in Transcaucasia.

Leaves with fewer than 8 stomata rows per band include seven specimens with 7 rows—from Germany, Austria, Switzerland, Bosnia, and Turkey; these belong to the *T. baccata* Alliance. Those with fewer than 7 rows were relatively rare (1–2% of 196 specimens cited for the Euro-Mediterranean Region), two specimens with 5 rows from Norway and Sweden, and one with 4 rows from Slovenia. These are considered *T. canadensis* as shown later. A cline is not apparent in the Euro-Mediterranean as it is in North America; however, the relative frequent occurrence of stomata in 8–10 rows per band appears significant when compared to a greater range of variation in E Asia (7–21 rows per band, Fig. 2C).

In E Asia, the number of stomata rows per band ranged from 7–16 in the temperate region, and from (5–) 7–19 (–21) in the tropical region with two patterns converging in the Himalayas, one from the west with 5–8 (–11) rows of stomata, and another from the east with 7–21 rows per band.

Number of Marginal Cells (MC).—The absence of papillae nearest the leaf margin, as measured by the number of marginal cells (MC) across between the margin and stomata band, is depicted geographically in Figs. 3A and 3B, and detailed in the Appendix.

Data on marginal cells lacking papillae along the abaxial surface (MC) were recorded less often for North American species because they were distinguishable early in the study (Hils 1993; Spjut 1992, 1993). It was recognized that marginal cells of *T. canadensis* always lacked papillae (Hils 1993, Spjut 1992, 1993, 1998a, 2000b), which has since been determined to vary from 11–19 cells across in North American plants (Appendix); the absence of papillae on the abaxial midrib is in sharp contrast to the papillose midribs of other North American species (*T. brevifolia, T. globosa*).

In the Euro-Mediterranean, the abaxial surface of leaves of most *Taxus* specimens (~75%) lacked-papillae along a relatively narrow marginal zone of 4–7 cells across (Fig. 3A). This included the lectotype for *T. baccata* and two specimens from the Caucasus Mountains that, unlike the lectotype, were found to have a relatively high stomata count as noted earlier—one with 13 stomata rows per band, and one with 15 stomata rows per band—and also one specimen from Bosnia with 12 stomata rows per band. A specimen from the Caucasus Mountains—that had abaxial marginal papillae to within one cell from the margin—lacked papillae on nearly half of the cells across the midrib in the median region (*Woronowa s.n.*).

Leaves of Euro-Mediterranean specimens with a relatively broad zone of bare cells between the margin and stomata band—from 8–24 cells across—were found less frequently (~25%). These are from widely scattered places. Many are indistinguishable from *T. canadensis* in North America—based on additional characters of branching, phyllotaxy, and color (Figs. 4–5); therefore, are referred to *T. canadensis* (Spjut 2000b). In Europe, leaves of *T. canadensis* may include a transitional zone of papillose cells between the stomata band and margin (Fig. 4, specimen from Morocco). These plants may be hybrids between *T. canadensis* and *T. baccata*.

The *Cuspidata* Alliance showed an intermediate range of values for abaxial marginal cells without papillae, (6–)8–18(–24) cells across (Figs. 3B, 6), compared to the *Baccata* Alliance, (1–)4–7(–11) cells across (Fig. 3A) and the *Sumatrana* Group, 8–36 cells across (Fig. 3B, 6). The higher stomata counts in relatively narrower stomata bands for the *Cuspidata* Alliance (see also Dempsey & Hook 2000) and *Sumatrana* Group means in effect they have a higher leaf stomata density, recognizing also that stomata density is related to width of the epidermal cells and the width of the stomata band (Nicolosi 1982), and that a transitional zone of papillose cells is always present in the *Baccata* Alliance but not in the *Cuspidata* Alliance. Data on number of papillose cells across the abaxial margin were not included in this study because this was observed to be highly variable, although the absence of papillae in *T. canadensis* has taxonomic significance in North American species as already indicated (Hils 1993; Spjut 1992, 1993, 1998a, 2000b).

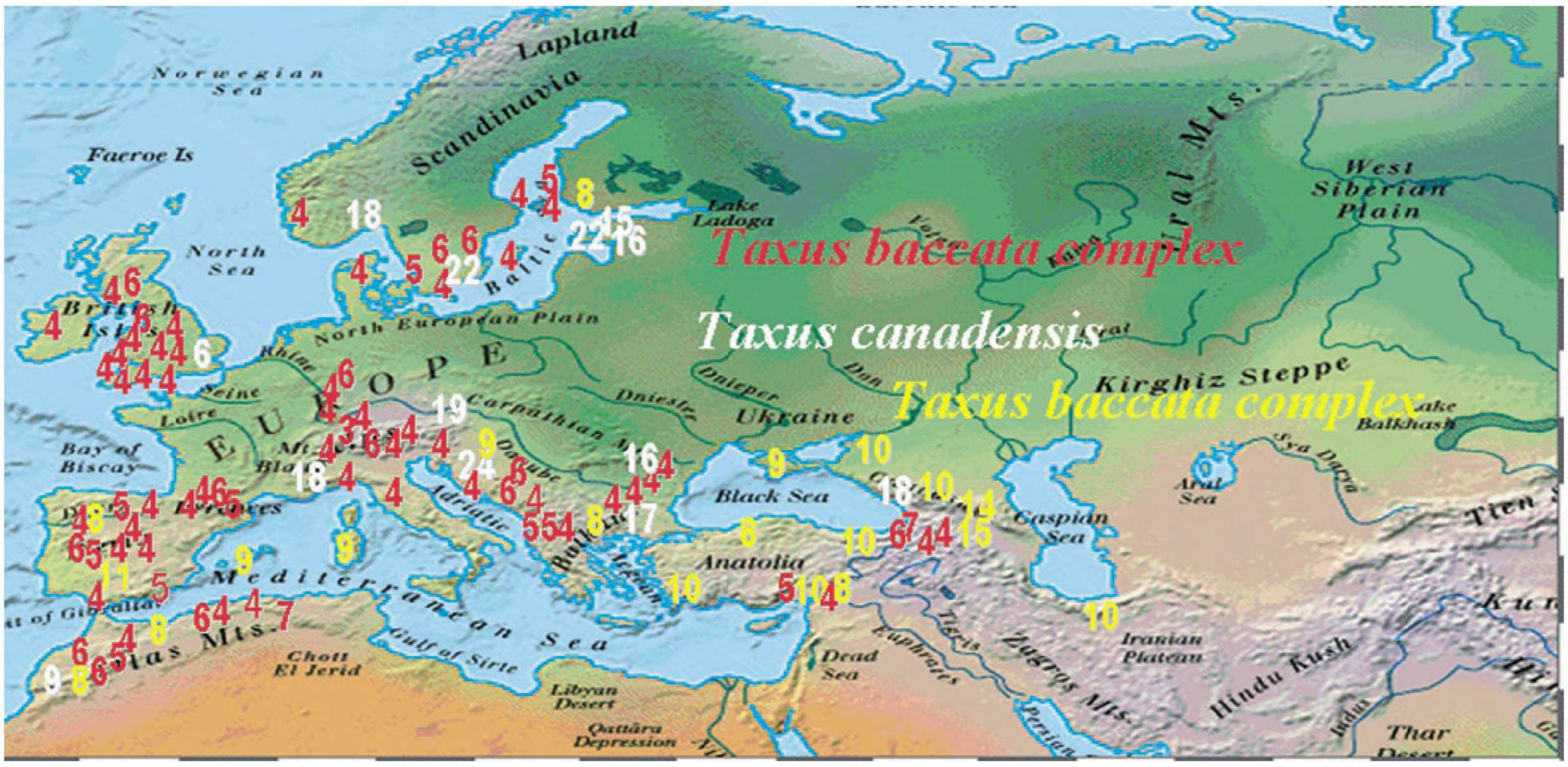


FIG. 3A. Number of epidermal marginal cells (MC) without papillae between the margin and stomata band (abaxial surface nearest margin) for representative specimens of *Taxus* from the Euro-Mediterranean Region; see Appendix for locality data. Numbers in red show the more common range in variation—a leaf margin 4–7 cells across—that corresponds to *T. baccata* and its allies in the Euro-Mediterranean Region. Numbers in white contrasts the higher counts—a leaf margin 6–24 cells wide—that belong to *T. canadensis*. Data in yellow numbers indicate intermediates that are morphologically similar to *T. biternata*, *T. canadensis*, *T. cuspidata*, or T. *contorta*, appearing more frequent in specimens from the Caucasus Mountains (Appendix, data in bold type)..

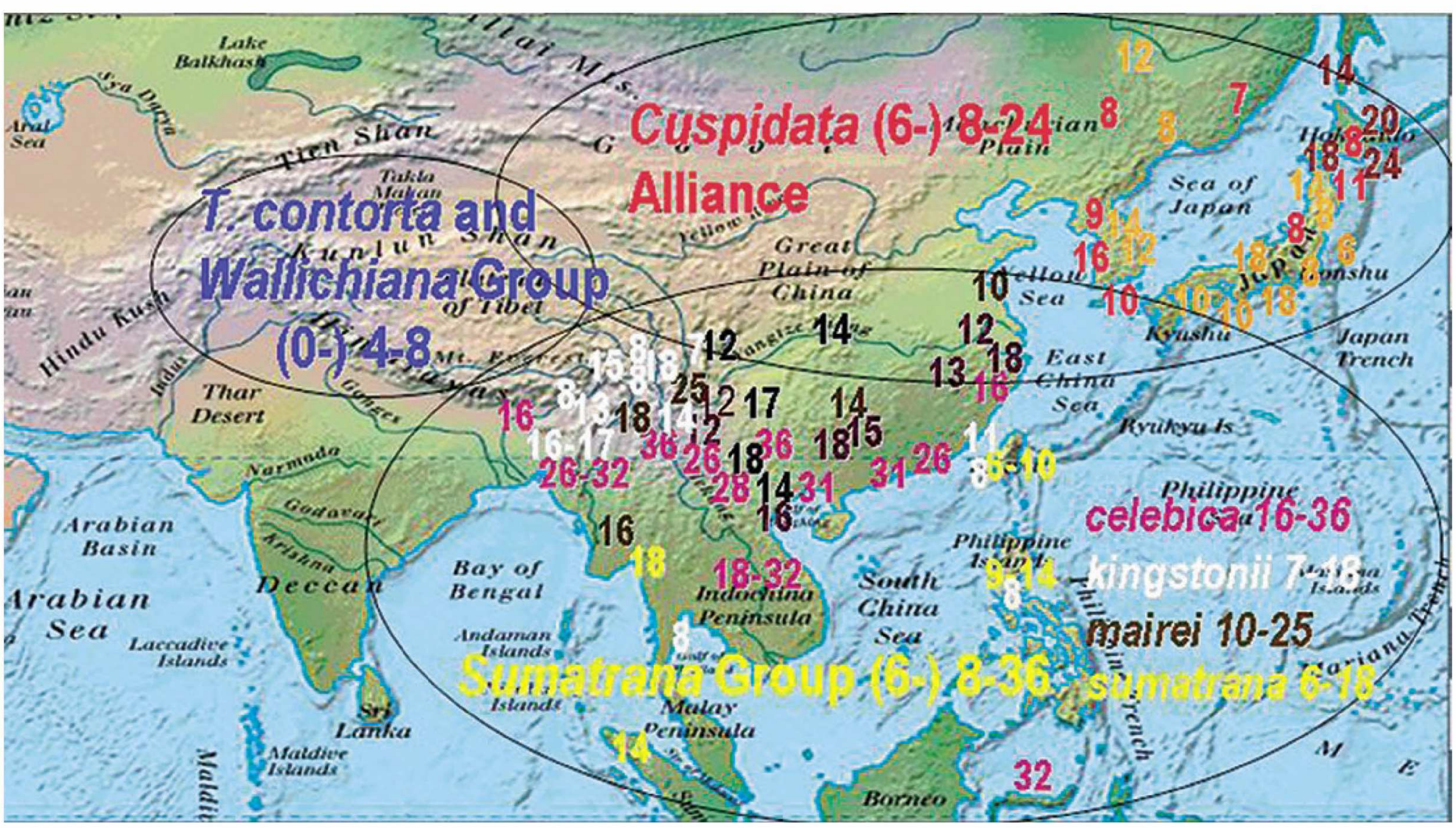


FIG. 3B. Number of epidermal marginal cells (MC) without papillae between the leaf margin and stomata band for three species groups of *Taxus* obtained from herbarium specimens cited in the Appendix. Data for the *Wallichiana* Subgroup and *T. contorta* (*Baccata* Group) are summarized, and data for the *Chinensis* Subgroup—summarized in Fig.6—are excluded here to further contrast the wide range in variation seen in the *T. cuspidata* Alliance (*Baccata* Group) and the *Sumatrana* Group. The *Sumatrana* Group includes *T. celebica* in maroon, *T. mairei* in black, *T. kingstonii* in white, and *T. sumatrana* in yellow. The *Cuspidata* Alliance includes *T. biternata* in orange, *T. cuspidata* in maroon, *T. caespitosa* and *T. umbraculifera* in red. Note that the widest range in variation occurs in SW China.

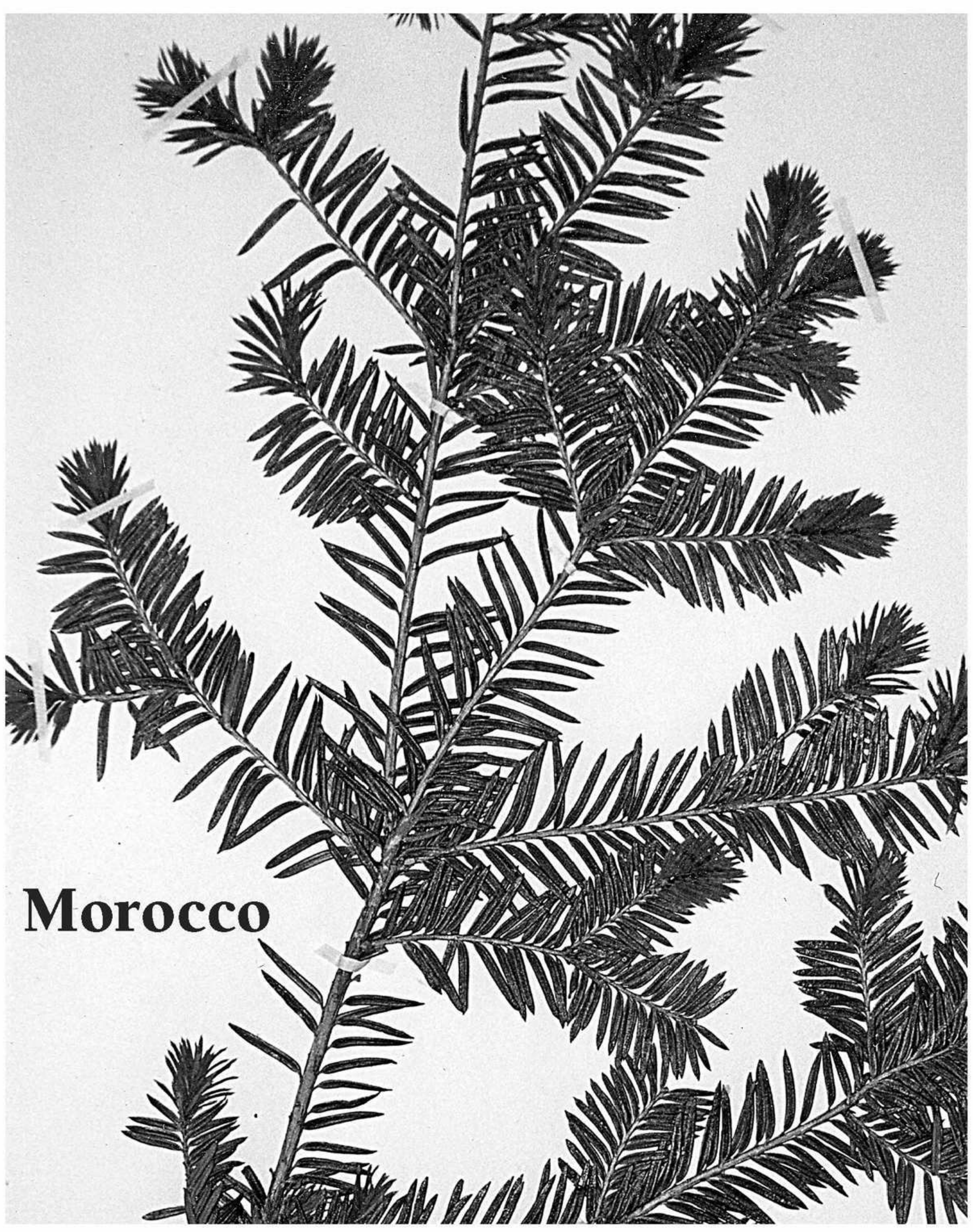


Fig. 4. Examples of *T. canadensis* var. *canadensis* as characterized by the regularly isodichotomous branchlets, and acute to acuminate leaves that spread from branchlets more by their petioles than by their blades, arranged in nearly two ranks, and by the abaxial surface of leaves lacking papillae on at least 8 cells across from the margin. MC = Marginal Cells across the marginal zone without papillae. SR = Stomata Rows in one stomata band. The specimen from Morocco has a partially papillose margin, 8–9 of the 18 cells between the margin and stomata band lack papillae. Specimens above left, above right and left: *Bean et al. 19634* (PH), *Lowe 570* (BM), *Font Quer 1928* (BM).

	Nova Scotia	Madeira	Morocco
MC	15	14	8-9(18)
SR	7	11	8

The absence of papillae along the abaxial marginal surface is most variable in E Asia (0–36 cells across, Figs. 3B, 6). This variation is related to taxonomic features that define the species groups and the species themselves as shown in Fig. 6. In Fig. 3B, the numerical data for the *Taxus wallichiana* Group, and for the NW Himalayan species, *T. contorta* (*Baccata* Group), were summarized because leaf stomata bands are consistently bordered by a relatively narrow marginal zone of epidermal cells without papillae—most often 4 cells across (Fig. 6)—as seen also in the *Baccata* Alliance (Fig. 3A, Appendix). Asian plants with a marginal border of fewer than 4 cells across generally belong to *Taxus wallichiana* var. *yunnanensis* (W.C. Cheng & L.K. Fu) C.T. Kuan, or to *T. suffnessii* Spjut, whereas specimens with an abaxial leaf margin exceeding 7 cells in width usually belong to the *Sumatrana* Group and *Cuspidata* Alliance, but there are several notable exceptions. One is *Taxus chinensis* with a leaf margin of 4–12 cells wide that is clearly intermediate between the *Sumatrana* Group and the *Cuspidata* Alliance, corresponding also to its intermediate geographical posi-

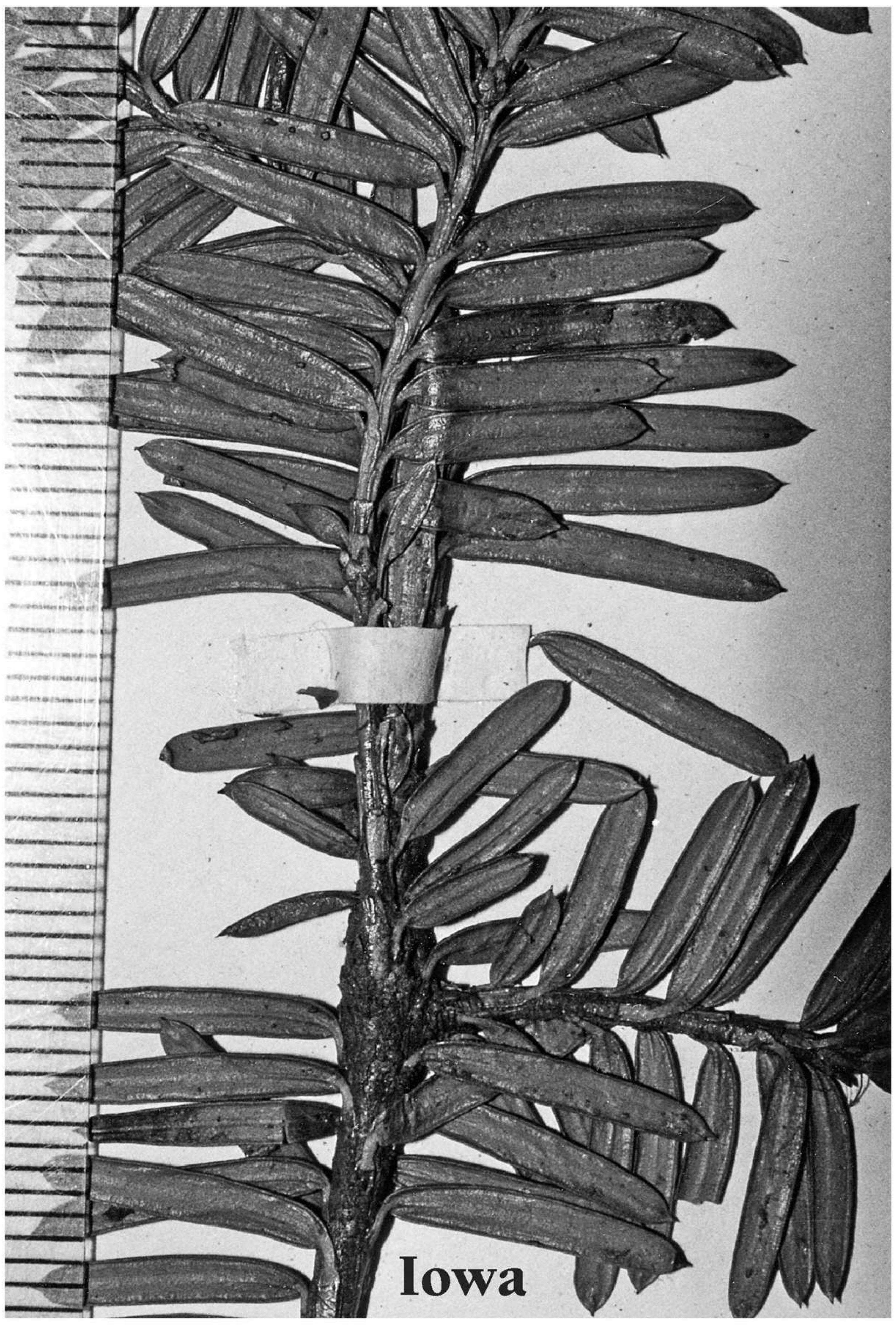


Fig. 5A. Examples of *T. canadensis* var. *adpressa* from North America and Europe. MC refers to number of cells without papillae between the margin and stomata band. SR refers to the number of stomata rows in a stomata band. Specimens from left to right: *Fink s.n.* (US), *Anderson s.n.* (US: 1091452), *Asplund s.n.* (US), and *Berglund s.n.* (S: C-2066).

	Iowa	Norway	Sweden	Slovenia
MC	12-15	18	22	24
SR	6	5	5-8	4-6

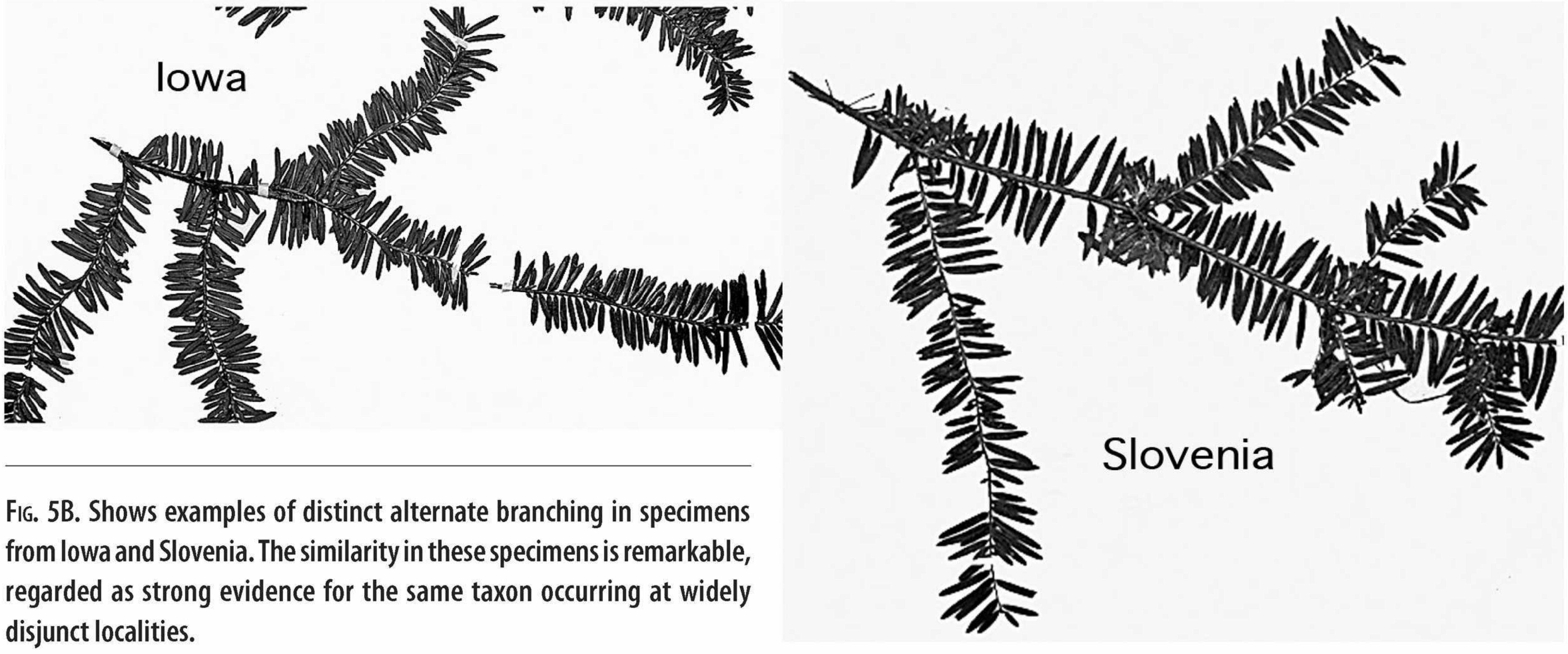


Fig. 5B. Shows examples of distinct alternate branching in specimens from Iowa and Slovenia. The similarity in these specimens is remarkable, regarded as strong evidence for the same taxon occurring at widely disjunct localities.

tion in central China. Another is the central Himalayas *T. contorta* var. *mucronata* Spjut, a variety that is recognized by shorter reflexed leaves as in *T. umbraculifera* (*Cuspidata* Alliance) but also with slightly more stomata rows per band (8–11) and a wider leaf margin (8–10 cells across) than what is usually seen in the typical variety of NW Himalayas.

Data in Figs. 3B and 6 also contrasts the wide variation in the number of marginal cells in the *Sumatrana* Group and *Cuspidata* Alliance with other Asian taxa. The *Sumatrana* Group and *Cuspidata* Alliance share the elliptical shape of epidermal cells as seen in T-section, in contrast to the angular leaf epidermal cells of the *Wallichiana* Subgroup, and also lack of papillae on the abaxial midrib as well as along marginal regions (e.g., *T. sumatrana*, Fig. 1C). This group usually occurs at elevations below 2000 m in contrast to *T. wallichiana* found mostly above 2300 m. One exception, *T. kingstonii* Spjut, in the *Sumatrana* Group, is ecologically and morphologically intermediate between the *Wallichiana* and *Sumatrana* Groups.

Variation in the number of abaxial marginal cells recorded from the same plant, or related plants at the same locality, was assessed similarly to data compiled on number of stomata rows. Among duplicate herbarium specimens, the count was the same in nearly half of the duplicate sets. Most variation within individuals, or within a population of individuals, occurred in the *Sumatrana* Group (*T. celebica* [Warb.] H.L. Li, *T. kingstonii, T. mairei* [Lemée & H. Lév.] S.Y. Hu ex T.S. Liu*, T. sumatrana*; Fig. 3B, Appendix). For example, leaves from duplicate specimens of *T. mairei* from Guangdong often lacked papillae along the abaxial margin on either 14 or 24 cells across. Similar dimorphic differences are evident in specimens from Sichuan and Guizhou, and in *T. kingstonii* from Yunnan. These differences may be due in part to leaves from different plants, or from different ages of shoots, or from different heights on the plant (de Laubenfels 1988), or in *T. celebica*, from slightly different regions of the leaf.

In the case of *Wilson 1265* (A, BM, K, S, US), which was mentioned earlier as having been collected from three different locations (Rehder & Wilson in Sargent 1914), one site in western Sichuan at 600–650 m included duplicate specimens that was found to have either 15 (US) or 21 (A) stomata rows per band, and either 16 (US) or 25 (A) marginal cells. *Wilson* also collected seed (*Wilson 1265*) from Sichuan near Mt. Emei and/or Yachou Fu at 600 m from which leaves in three herbarium specimens obtained from a plant grown from seed (of *Wilson 1265*) at the Royal Botanic Gardens—Kew lacked papillae entirely along an abaxial margin zone, 18 or 28 cells across, while all three had 8–10 stomata rows per band. This plant is not *T. chinensis* as indicated in the literature (Rehder & Wilson in Sargent 1914), but *Taxus mairei* var. *speciosa* (Florin) Spjut that appears atypical by the relatively large greenish distant leaves that are more characteristic of *T. celebica*. Photographs of a very similar plant in cultivation at the Royal Botanic Garden—Edinburgh (probably from *Wilson 1265* seed) are shown in van Gelderen and van Hoey Smith (1996) and in Krüssmann (1985). However, *Wilson 1265****(b)*** does include one specimen I identified as *T. chinensis* that was reportedly obtained from western Hubei south of "Ichang," 600–1300 m.

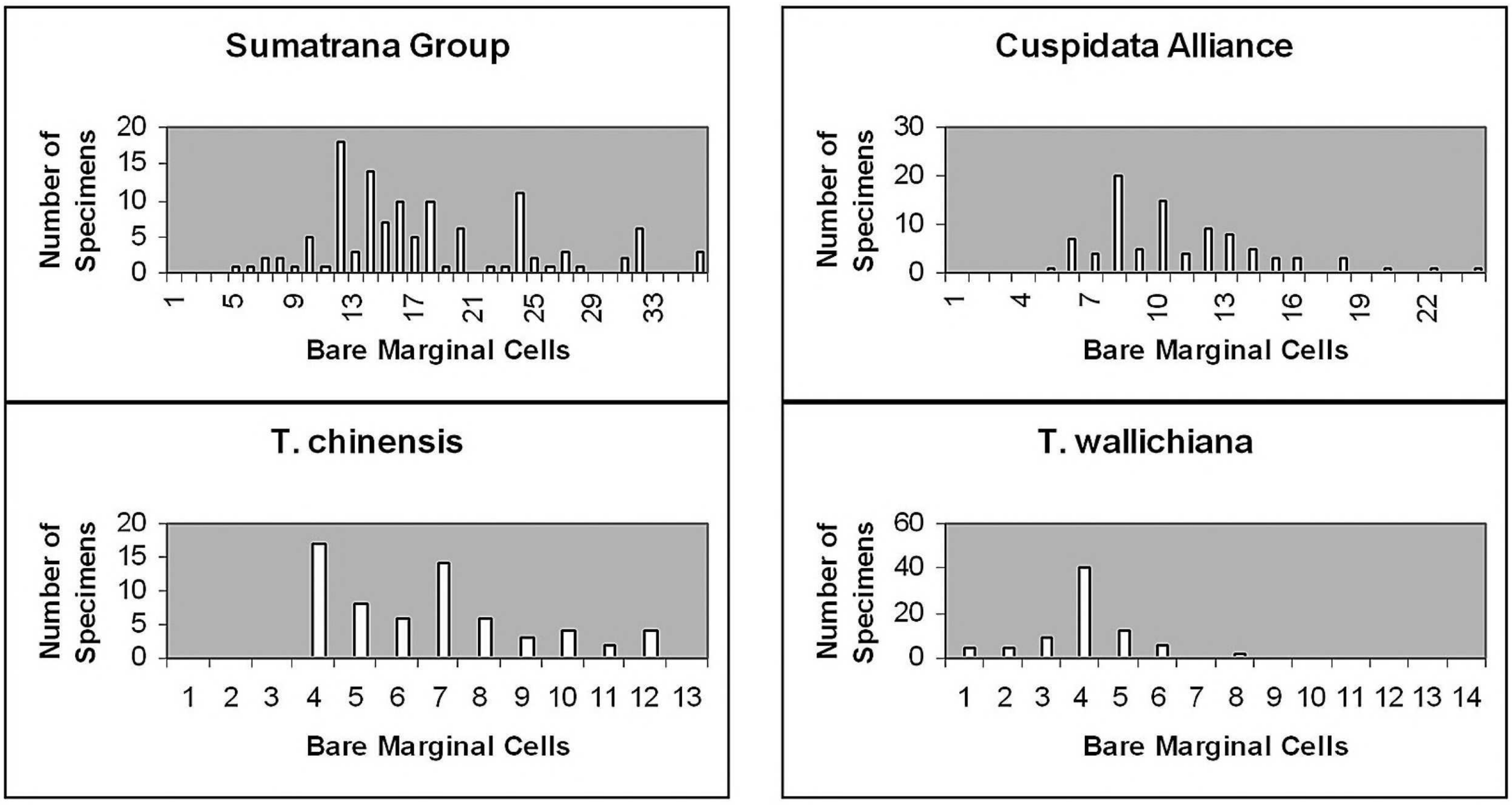


Fig. 6. Number of *Taxus* specimens according to the number of bare (without papillae) cells across abaxial surface of leaves between the margin and stomata band for selected taxa from E Himalayas to China. Note that the *Sumatrana* Group has the widest leaf marginal zone without papillae, and that *T. wallichiana* has the narrowest zone, mostly 4 cells wide (40 specimens).

De Laubenfels (1988), commenting on his field observations of yews in Taiwan, suggested that differences in leaf shape may be seen on the same plant and further implied the same for the presence or absence of leaf papillae.

Leaves of *Taxus mairei* var. *speciosa* that showed considerable variation were also studied from plants cultivated in the United States. An examination of 20 leaves (*Phyton s.n.*)—from apical buds to 3rd yr branchlets—were found to be relatively constant in the number of marginal cells without papillae—9 cells across—and also in having 16–18 stomata rows per band. They were notably variable in shape and length of epidermal cells, especially juvenile foliage.

The abaxial leaf margin in *T. mairei* specimens obtained by C-j. Chang from near Hualien, Taiwan varied by four cells (4–7) at four of six locations (Nos. 2, 4, 9, 10), and by only two cells (0–1 cell) at the two other locations (Nos. 1, 5).

Finally, specimens of *T. celebica* from South Vietnam by Schmid (1974) were found to lack papillae on either (23–) 24 or 32 cells across the leaf margin. Here Schmid (1974) reported that *Taxus* was polymorphic, and among his specimens at the Museum of Natural History in Paris (P), is an apparent hybrid (*Schmid s.n.*) between *T.* aff. *chinensis* (*Poilane 4150*) and *T. celebica.*

DISCUSSION

Phytogeography of *Taxus*.—Data presented for leaf character attributes of *Taxus* (Figs. 2 and 3) show that stomata rows and marginal cell features are most diverse in SW China, while the same number of subspecies (Pilger 1903), or species (Farjon 1998; Silba 1984) have been recognized to occur in both North America and Eurasia; thus, the traditional separation of *Taxus* species (or subspecies) based on these geographic discontinuities is a distorted classification. The phytogeographic data in this study support the taxonomy of yew for only the geographical disjunct occurrences in North America.

In North America, leaf stomata of *Taxus brevifolia* show a cline in number of stomata rows ranging from 9 rows in California to 4 rows in the northern Rocky Mountains, and also in length of abaxial epidermal cells relative to width (l/w) from an average of ca. 3× l/w to 8× l/w. Molecular differences have been reported between coastal and inland yews (El-Kassaby et al. 1994, 1995) at more northern localities. Clinal variation in conifers has been linked to historical migrations and hybridization patterns with the advance and retreat of glaciers since the Pliocene (Wilkinson et al. 1971); however, the cline in stomata data for the North American *Wallichiana* Subgroup, including Mexico, seems best explained by loss of stomata in leaves of *Taxus* as it may have migrated northwards during the Neogene, when the climate may have become increasingly warmer and drier, while the differences within the Pacific Northwest may be a product of more recent climatic changes (Graham 1999).

Also, a geographical species concept that recognizes *T. sumatrana* as widely distributed in SE Asia (de Laubenfels 1988) might conclude that its distribution was achieved from long-distance dispersal by birds, whereas geographical disjunction of *Taxus* in North America has been correlated with paleobotanical data (Graham 1999). This seems paradoxical; i.e. the greater variation in leaf anatomical data of *Taxus* in Asia should also be explained by evolution and paleogeography—perhaps the result of climatic and geomorphic changes that have occurred since the Cretaceous, a period of 130 million years (my). Therefore, the discussion that follows will focus on this latter hypothesis.

Although data on leaf stomata rows in *Taxus* are more variable in Asia than in North America and Europe, relationships become evident when other taxonomic features are taken into consideration (Spjut 2007). For example, in the western Himalayas, the stomata counts that range from 5–8 (–10) or 8–11 stomata rows per band (Fig. 2C) are a characteristic feature of *T. contorta* Griff. This species is also recognized by the long narrow leaves that have idioblasts in the spongy mesophyll (vesicular cells appearing dark red in herbarium specimens), a character trait not seen in the E Himalayan yews. Moreover, these features show a closer relationship to European yews than to Asian yews. In the E Himalayas, *T. wallichiana*—indicated to have 11–19 stomata rows—is recognized by leaves having large angular shaped epidermal cells as seen in T-section, by the persistent bud-scales at the base of branchlets, by the branchlets that show a marked color change in their 2nd yr of growth—from yellowish green to maroon or reddish orange, and by the bone-like parenchyma cells in the spongy mesophyll that connect in a reticulate pattern with rounded to angular intercellular spaces. These morphological features are considered more closely related to yews of SW China than to *T. contorta* of W-C Himalayas.

Data in the appendix take into account variation in *T. chinensis* and *T. wallichiana* on Mt. Emei. Specimens are arranged according to increasing number of marginal cells along the abaxial surface of the leaf without papillae. In *T. wallichiana*, the epapillose marginal cells, which are consistently 4 wide for numerous specimens in the Himalayan Region (see also Fig. 10 in Spjut 2007), appear to show greater variation on Mt. Emei where it was found that two of six specimens had a leaf margin 8 cells wide. Similarly, *T. chinensis* outside of Mt. Emei was usually found to have a relatively narrow leaf margin of 4–7 cells wide, 25 of 30 specimens (83%); only 2 specimens (7%) were found with a leaf margin greater than 8 cells wide, whereas on Mt. Emei, 11 of 30 specimens (37%) had a relatively broad leaf margin (8–12 cells across). The broader leaf margin in *T. chinensis* from Mt. Emei could be the result of recent hybridization with species of the *Sumatrana* Group, or possibly reflects historical introgression with *T. umbraculifera* of NE China. Hybridization might also account for similar variation in *T. chinensis* for three specimens from Guizhou, Shaanxi, and Vietnam.

The development of leaf papillae in *Taxus* along the abaxial marginal zone may be partially correlated with latitude as evidenced by the narrower range of marginal cells without papillae (7–24 cells across, Figs. 3B, 6) for the *T. cuspidata* Alliance in temperate NE Asia, compared to that of the more widely distributed *Sumatrana* Group (8–36 cells across, Figs. 3B, 6) in SE tropical Asia. At increasingly higher latitudes, plants with more papillae on their leaves obviously receive greater protection from ultraviolet rays of the sun—during the longer summer days. The refractivity (protective) effect of papillae on *Taxus* leaves has indeed been mathematically demonstrated (von Frimmel 1911). Nevertheless, hybridization between the tropical and temperate species alliances in E Asia cannot be ruled out.

In the *Cuspidata* Alliance, I have observed that papillae are of lower stature and concrescent near cell walls in which the cell walls appear thicker, examples of which are shown in Jinxing and Yuxi (2000). This may be evidence of introgression with the *Wallichiana* Group from which *T. chinensis* allegedly evolved. As indicated, leaves of *T. chinensis* often have elliptically shaped epidermal cells in T-section, a slightly wider marginal border, ranging from 4–12 smooth cells across (Fig. 6), and midrib papillae often more conspicuous along cell walls. Thus, the *Cuspidata* Alliance, which is undoubtedly related to the *Baccata* Alliance (Collins et al. 2003; J. Li et al. 2001), may have acquired an expanded leaf margin as a result of hybridization with species of the *Sumatrana* Group.

In cultivated individuals related to *T. cuspidata* and *T. mairei*, papillae sometimes were found on midribs of young leaves, but not the older leaves. However, the odd leaf mentioned earlier for one cultivar (*T. caespitosa*) with 16 instead of 13 stomata rows/band was found with low papillae on its midrib, whereas the other 15 leaves had smooth midribs; this odd leaf may have retained juvenile characteristics due to lack of exposure to light. I have also completely "skinned" leaves to evaluate the distribution of papillae from base to apex in specimens from Europe, Taiwan and the Philippines, and have found papillae to develop more in the upper half (towards apex). The presence of midrib papillae on juvenile leaves, thus, may indicate an ancestral trait that should not be treated as a justification for lumping all variation within a geographical area under one species.

This alleged ancestral trait is also evident among specimens that are intermediate between *T. chinensis* and *T. mairei*, and the extinct *T. engelhardtii* (Fig. 7). The characteristics of *T. mairei* include larger (mamillose) epidermal cells on the abaxial midrib and marginal zones, and isodichotomous zigzag branching; those of *T. chinensis* are the marginal papillae on the abaxial midrib [e.g., *Ching 1676* from Sichuan; *Chiao & Fan 464* (US) from Sichuan, and *Tsiang Ying* 1425 (P)]. A study by Kwei and Hu (1974)—that mentioned 30 of the specimens cited in the Appendix—recognized intermediates by a partially papillose midrib; however, Spjut (1992, 1993, 1998a) has since reported other correlative taxonomic characters—such as shape of leaf epidermal cells, development of papillae along the abaxial marginal zone and size of bud-scales—to help further separate these species. It should also be noted that midrib papillae can be consistently present in the W Himalayan *T. contorta* (Kvaček 1984), or consistently absent in the North American *T. canadensis*.

From Myanmar are four specimens found to have leaves almost entirely papillose within a few cells from the abaxial margin. Three of the specimens are recognized as belonging to a distinct species (*T. suffnessii*) by the relatively large and persistent bud-scales at base of branchlets, by the conspicuous papillae on epidermal cells, and by the relatively tall-rectangular epidermal cells as seen in T-section of leaves (Spjut 2007). One of two other specimens from NE India and Bhutan (*Ludlow & Sherriff 18762, 3719*)—that was recorded to be papillose within 2 cells from the margin—differed by having elliptical instead of angular epidermal cells. It would appear, then, that the occurrence of papillae on the abaxial surface of *Taxus* leaves has taxonomic significance even when the numerical differences are relatively narrow as also seen in North American *T. globosa* var. *globosa* and *T. globosa* var. *floridana* in which intermediates are recognized to occur in northern Mexico.

Disjunct Relationships between Eastern Asia and Western North America.—Disjunct geographic distributions in *Taxus* and other genera have long been recognized between temperate North America and Eurasia (Axelrod 1983; Boufford & Spongberg 1983; Good 1964; Graham 1972; Hara 1972; Kornas 1972; H. Li 1952; Tiffney 1985a; Qian 2002; Q. Wang et al. 2006); however, their rate of evolution varies. For conifers this has been considered relatively slow (Prager et al. 1976). In the genus *Abies,* for example, the subalpine fir in W North America [*A. lasiocarpa* (Hook.) Nutt.] appears more closely related to an endemic species of Taiwan [*A. kawakamii* (Hayata) Ito] than to any of the 10 other American species (Farjon 1990; Hunt 1993; Liu 1971). Indeed, recent molecular studies by Suyama et al. (2000) show *A. mariesii* Masters of Japan to be more related to species in North America than to its relatives in Japan. Additionally, species of *Pseudotsuga* (±4 spp., Farjon 1990) in Asia may have been derived from ancestors in North America (Strauss et al. 1989).

The *Wallichiana* Subgroup of *Taxus*—characterized by angularly shaped epidermal cells in T-section—occurs primarily in E Himalayas to SW China (Sichuan, Yunnan) and in North America (Spjut 1998a, 1998b, 2000a). Within this subgroup, leaves of Yunnan and Sichuan plants (*T. florinii,* Spjut) appear indistinguishable from those of the American *T. globosa* (Spjut 1998b, 2000a, 2000c). Other specimens from Myanmar

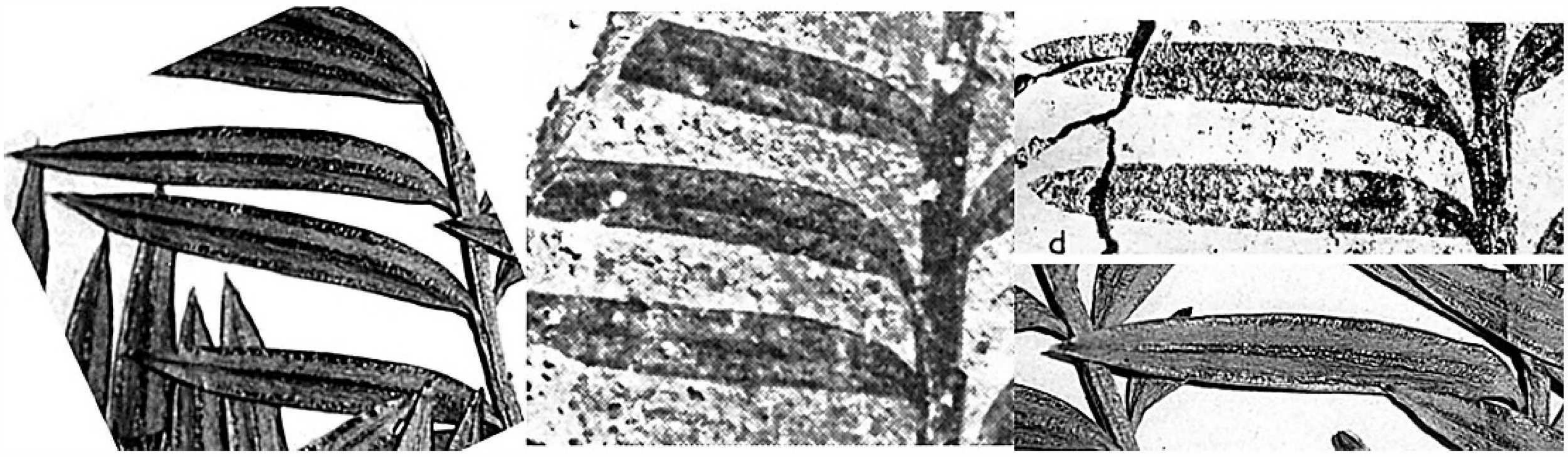


Fig. 7. Comparison of leaves of extant *T. mairei* (clear photos, isotype, P) with extinct *T. engelhardtii* (grainy photos, reproduced from Kvaček 1984), from an Oligocene deposit in Bohemia.

(*T. suffnessii*) are similar to *T. brevifolia* in the relatively large bud-scales and tall rectangular epidermal cells as seen in T-section (Spjut 2000c).

An analogous disjunct relationship is seen among the white pines, *Pinus monticola* Douglas ex D. Don of W North America and *P. wallichiana* A. B. Jackson of Myanmar (Axelrod 1986, *Pinus griffithii* [Hook. f. & Thomson] Parl.). They are remarkably similar in cone morphology and needle chemistry. The antiquity of this relationship is supported by their turpentine chemistry of saturated straight chain hydrocarbons—undecane and heptane, the chemical structures of which are considered more archaic among the terpenoid compounds in pines (Mirov 1953). Additionally, heptane occurs in the Mexican *P. ayacahuite* Ehrenb. ex Schltdl. (Mirov 1953), along with a bicyclic sesquiterpene—cardenine—that has also been found in *P. parviflora* Siebold & Zucc. of Japan (Mirov 1953). The close relationship among these species, which belong to sect. *Quinquefoliae* subsect. *Strobus*, is supported by molecular data (Liston et al. 1999) from which it has been suggested that the ancestors probably originated in the "Old World" (Gernandt et al. 2005).

In angiosperms, it is interesting that Phipps (1983) recognized—among ~145 species of hawthorns—*Crataegus mexicana* Moç. & Sessé, a widely distributed species in Mexico and Guatemala, to have its closest relative in Yunnan, *C. scabrifoliaI* (Franchet) Rehder, and that both are the "most primitive" of a taxonomically complex Laurasian genus, which has numerous species in both Mexico and in Yunnan.

For taxads and other conifers, diversity is greatest in SW China (Figs. 2, 3; Cheng & Fu 1978; Prakash et al. 1995; Qian & Ricklefs 1999). Ancestors related to *Taxus suffnessii* Spjut in Myanmar (Appendix) may have immigrated to North America across a former Aleutian (or Bering) land bridge (Hamilton 1983; Millar 1993)—as suggested for *Crataegus* (Phipps 1983). A logical time for this to occur would have been during the latter half of the Cretaceous (110–100 mya), after Pangaea had fragmented (Graham 1993)—when an epeiric sea (Wolfe 1975) possibly divided the North American continent into distinct west and east floras (Graham 1999; Srivastava 1994; Thorne 1972, 1978). Late Cretaceous fossils related to the Alaska cedar, *Callitropsis nootkatensis* (D. Don in Lambert) Florin, which includes one related sister species in North Vietnam, and is also sister to other species in North America (Little 2006), have been found on Vancouver Island (McIver 1994), and an early Cretaceous fossil, *Chamaecyparis eureka* Kotyk, from Eureka Sound in the Canadian Arctic, is most similar to the extant *Ch. pisifera* Siebold & Zucc. in Japan (Kotyk et al. 2004). Additionally, fossil cones of *Thuja smileya* LePage from Late Cretaceous deposits on the North Slope of Alaska are indistinguishable from modern species (LePage 2003).

As climate temperatures declined during the Cretaceous (Axelrod 1958; Frederiksen 1994; Graham 1999; Novacek 1999; Srivastava 1994), *Taxus* might have retreated southwards, perhaps reaching southern Mexico by the end of the Cretaceous (65 mya); similar retreats have been suggested for other genera (Phipps 1983; Sharp 1966), but for the Tertiary Period (Phipps 1983), not the Cretaceous. A later migration and extinction of *Taxus*, such as in the Tertiary near the Eocene-Oligocene boundary, may seem like a more reasonable time frame for evolution of North American *Taxus*, but there also has to be ample time for diversification of the *Cuspidata* Alliance as well as the alleged migration and extinction of the *Wallichiana* Group across the Sino-Japanese Region.

The end of the Cretaceous is marked by a distinct change in the geochemical and fossil records (McIver 1999; McIver and Basinger 1999; Novacek 1999)—indicating a rapid climatic warming—possibly due to a meteor impact in the Caribbean Sea that might have caused massive volcanic materials to erupt and cloud the atmosphere (O'Keefe & Ahrens 1989)—a 'greenhouse' calamity that could explain evidence for "ecological deserts" (Tschudy et al. 1984)—and mass extinction of major taxa (e.g., dinosaurs, Novacek 1999). This could have extirpated yew north of Mexico; Cretaceous fossils of gymnosperms of the Taxodiaceae (*Metasequoia, Sequoia, Sequoiadendron*), and Amentotaxaceae (*Amentotaxus, Torreya*) are known as far south as New Mexico and North Carolina (Florin 1963) for which *Taxus* has had a long history in association (Florin 1951, 1963; Kvaček 1984) but whose fossils may not always be preserved or identified.

Paleontological evidence indicates that following the Cretaceous a warmer subtropical humid climate (Chaney 1947; Frederiksen 1994; Tiffney 1985a) prevailed over much of North America until the late Eocene (ca. 50 mya; Chaney 1947; Graham 1999; Novacek 1999; Srivastava 1994; Wolfe 1975). Assuming that ancestral *T. globosa* had survived only in Mexico, a northward migration (as the climate warmed) would account for the cline in leaf stomata data of *Taxus* in W North America (Fig. 2A). Other North American conifers with evidence of a southern ancestry include Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), most likely derived from big cone fir (*P. macrocarpa* (Vasey) Mayr), endemic to S California (Strauss et al. 1989), and pines that may have drifted northwards on the San Andreas rift system (Axelrod 1986)—a system that may have included Vancouver Island originating perhaps from as far south as "lands end" off the cape (Cabo San Lucas) of Baja California (90 mya, Ward et al. 1997). A northward range extension of ancestral *Taxus globosa* may be further correlated with the change in a Rocky Mountain flora from paleotropical (boreotropical) to neotropical elements during the mid Eocene (Leopold & MacGinitie 1972), and later along the Gulf as evident from biogeographical data on fishes and amphibians (Rosen 1975), maples (*Acer saccharum* L. Group; Humphries 1982), and other taxa (Burnham & Graham 1999)—emphasized by Axelrod (1975, 1986).

As the climate became drier with the uplift of the W Cordillera (Chaney 1947; Wolf 1969), the range of *Taxus*, like other Arcto-Tertiary genera, diminished (Axelrod 1975, 1983; Graham 1993, 1999), while other taxa evolved (Axelrod 1958). Fossils of *Taxus* have been reported in Eocene (54–38 mya), Oligocene (38–27 mya), and Miocene (27–10 mya) strata of W North America (Gaussen 1979; Kvaček & Rember 2000, in press; Manchester 1994; Meyer & Manchester 1997) in association with species of *Tsuga, Abies, Lithocarpus, Quercus, Acer, Alnus, Cornus, Carpinus, Castanea, Fagus, Liquidambar, Nyssa, Ostrya, Platanus, Tilia, Ulmus*, and *Cercidiphyllum* (Graham 1999; Whittaker 1961).

Extant species of *Taxus* are still found with these same genera today in mixed mesophytic forests of S Appalachia (Braun 1950), China (Hou 1983), and Japan (Hayashi 1954). *Taxus brevifolia* allegedly evolved from an ancestral *T. globosa* complex as the climate became cooler and drier during the Eocene (56–34 mya; Graham 1999), while closer ties between the Mesoamerican yew and Florida yew were likely maintained until the Pleistocene as evidenced by the close similarity among many shared taxa between the two regions (Sierra Madre Oriental and S Appalachia). It is interesting that specimens of Florida yew appear indistinguishable from those occasionally collected in Veracruz and in Nuevo Leon/Tamaulipas, Mexico (e.g., *Meyer & Rogers 2746*, BM; *Mueller 1337*, BM, PH), where they reportedly occur with *Carpinus caroliniana* Walter, *Cercis canadensis* L., *Frangula caroliniana* (Walter) A. Gray, *Hamamelis virginiana* L., *Liquidambar macrophylla* Oerst, *Magnolia schiedeana* Schltdl., *Prunus serotina* Ehrh, and others also found in S Appalachia, including many lichens and mosses (Culberson et al. 1990; Graham 1973, 1999; Miranda & Sharp 1950). Moreover, it has been shown that the Florida yew and Mesoamerican yew form a clade with the Pacific yew as a sister species (J. Li et al. 2001), and that the Florida and Mesoamerican yew are indeed more closely related (J. Li et al. 2001).

As previously noted, genera found with the Mesoamerican yew also occurred with Pacific yew (Graham 1999), but in the Pacific Northwest many of these genera perished—such as *Carya, Disopyros, Fagus, Hamamelis, Liquidambar, Liriodendron, Magnolia,* and *Morus* (Axelrod 1975, 1983, 1986; Graham 1999; Manchester

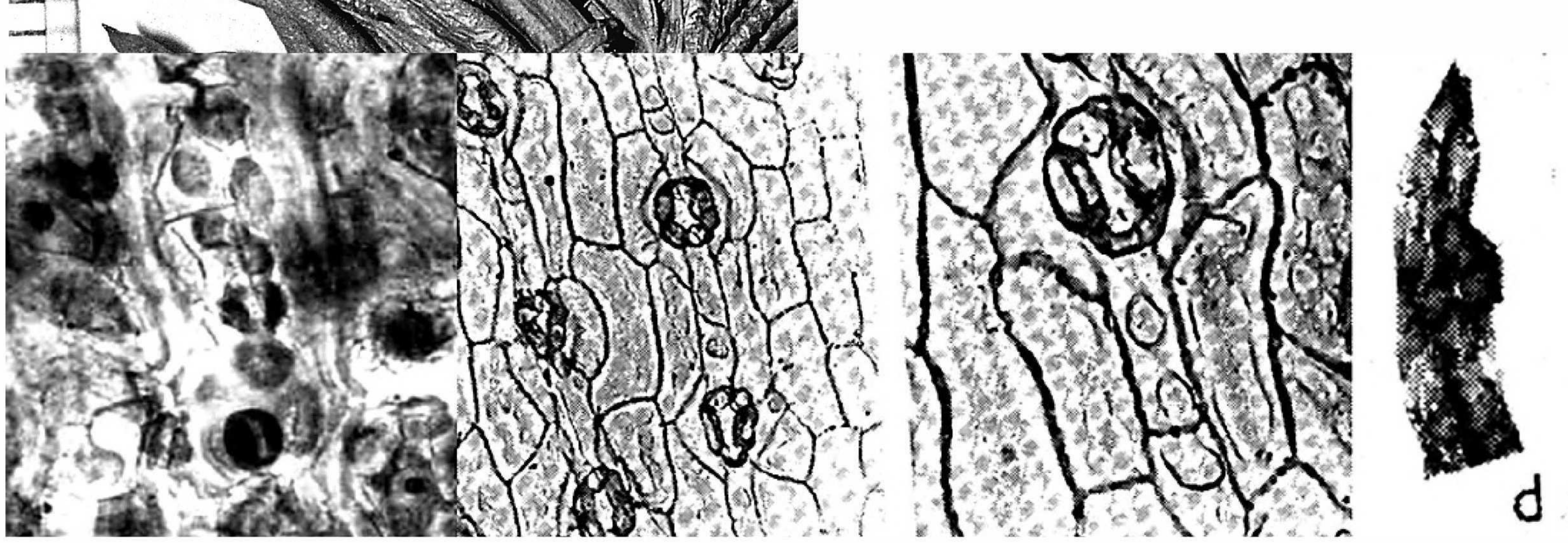
1999; Wood 1972). *Liriodendron* is one of many known from fossils in Europe and W North America with relatives now surviving only in E North America and E Asia (Axelrod 1983; Manchester 1999; Schuster 1976). They perhaps were part of a widespread Tertiary "boreotropical" forest (Wolfe 1975; Graham 1999), which may have included *T. canadensis* (Figs. 4, 5).

As conifer diversity declined and grassland vegetation expanded during the Miocene (Axelrod 1976; Jacobs et al. 1999), *Taxus* possibly had attained maximum diversity in geographic and ecological species isolation. McIver and Basinger (1989) found in Eocene deposits cones similar to western red cedar (*Thuja plicata* Donn ex D. Don) that may have been derived from an earlier complex related to the extinct *Thuja polaris* McIver *et* Basinger, which they described from a Middle Paleocene deposit on Ellesmere Island, whereas other cedars related to *Th. occidentalis* L. are not known before the Miocene (McIver and Basinger 1989). Moreover, *Th. occidentalis* is recognized in the fossil record from the late Pliocene (Bennike 1990). The redwood, *Sequoia sempervirens* (Lamb. ex D. Don) Endl., is hardly distinguishable from a former widespread *S. abietina* (Brongn.) Knobloch—known from the Upper Eocene to Upper Miocene (Mai 1998). A species of *Taxus* from a Middle Miocene deposit in N Idaho (Clarkia area Latah Formation) has nearly the same abaxial epidermal features seen in the extant *T. brevifolia* (Kvaček & Rember 2000, in press). Klicka and Zink (1997) concluded from DNA evidence that North American species of song birds had already originated by early Pleistocene, and that subsequent glaciation was more of an "obstacle course" for their survival. Yew species, by comparison, are likely to evolve more slowly as a yew trunk may live 3000 years (Larson et al. 2000; Thomas & Polwart 2003; Voliotis 1986), and still may survive by producing trunks from adventitious shoots (Hageneder 2007; Loudon 1844). The greater diversity of *Taxus* in SW China may also be related to less species extinction there as seen in many plant genera as a result of increasingly drier and cooler climates that had a more profound impact on the vegetation elsewhere since the Middle Miocene (Axelrod et al. 1998; Kubitzki & Krutzsch 1998).

Relationships between Eastern North American and Eurasian *Taxus*.—While the Pacific floristic element of *Taxus* in North America is represented by three disjunct taxa within the *Wallichiana* Group, the Atlantic floristic element has only *T. canadensis*, a species that appears more related to the *Baccata* Group (J. Li et al. 2001; Spjut 2007) than to *T. globosa* by its elliptical shaped epidermal cells in T-section, and by its subcylindrical seed shape (Spjut 1998a, 2000). The lack of papillae on the abaxial leaf surface between the margin and stomata band that characterizes the North American Canada yew is also seen more frequently in yews of temperate NE Asia (*Cuspidata* Alliance) than in the Euro-Mediterranean (*Baccata* Alliance), and its leaf epidermal features are most similar to *T. biternata* Spjut, a species closely allied to *T. cuspidata*. The close relationship between *T. canadensis* and *T. cuspidata* is supported by molecular data (Collins et al. 2003). *Taxus biternata* differs from *T. canadensis* by the 2–3 angled seeds (tapered part) developing on 1st yr branchlets, and by the tree habit (Spjut 2007). The complete lack of papillae along the abaxial leaf marginal zone is a relatively rare occurrence in European yew (<2%), but this character trait may have once been common in that region; for example, three species described by Kvaček (1984) from leaves of fossil assemblages in Europe—dating from Oligocene to Pliocene—all lacked papillae entirely between the stomata bands and margins.

Furthermore, a "*Taxus* (sp. 1," Kvaček 1984; Fig. 8) of Lower Miocene age is, in my opinion, *T. canadensis*. Its leaves are more similar to American plants than to European plants, which differ by the distinctly papillose stomata bands—except perhaps for rare North American specimens (e.g., *Coy & Glen* from Ithaca, New York). These extant European variants could be referred to the extinct *T. grandis* Kräusel or *T. inopinata* Givulescu (1973)—described from Tertiary deposits in Europe (Kvaček 1984). Data for numbers of stomata rows (Figs. 2A, 2B) also support my hypothesis that the North American *T. canadensis* came from Europe, possibly arriving late Paleocene or Eocene when migration across the Atlantic was possible by land (McKenna 1983; Tiffney 1985b), as suggested for the evolution of *Cornus sessilis* Torr. ex Durand (Xiang et al. 2005, 2006). During this period the Gulf Coast flora shows evidence of many immigrants from Europe (Frederiksen 1994, 1995) that included species of *Fagopsiphyllum, Hydrangea, Iodes, Koelreuteria, Langtonia, Nyssa, Palaeophytocrene, Pentoperculum, Platanites, Platycarya, Pyrenacantha, Sargentodoxa, Symplocos, Tapiscia, Tetraclinus*, and *Tilia* (Manchester

Fig. 8. Comparison of *T. canadensis* var. *minor* from Madeira (*Lowe ex Barby s.n.*, US) and Maine (*Fellows 5686*, US) above with close-up on middle left showing seed on 2nd yr branchlet, and below photomicrographs of part of leaf stomata band of var. *canadensis* from Ohio (400×) and of a Miocene fossil from Czech Republic ("*Taxus* sp. 1," Kvaček 1984) with leaf fragment ("d" on right). This variety is recognized by the more strongly falcate leaves that are mostly erect in contrast with the wide spreading obtuse leaves in var. *T. canadensis* var. *adpressa*. Note the medial papillae that are most conspicuous along stomata rows.



1999). It is interesting to note that 10 species (in 9 genera) of lichens recently discovered to occur in E North America—on Mt. Katahdin in Maine—were previously known only from northern and/or central Europe, except for one species that also occurs in Greenland and Siberia (Fryday 2006).

Relationships between the Euro-Mediterranean and Asian *Taxus*.—The European yews have all been considered a single species, *T. baccata*; however, additional species appear evident. The lectotype (of *T. baccata*) has leaves arranged mostly parallel to one other along two sides of a branchlet in a flat spray with 8–10 stomata rows/band and a papillose undersurface—from the midrib to near the margins. The typical European yew is further characterized by isodichotomous branching, pale glaucous green leaves similar in color on both surfaces, and cones maturing on branchlets that have terminated their growth as evident in specimens from England, Germany, Austria, Switzerland, Czech Republic, Spain, Portugal, Algeria, Morocco, Italy, Albania, Bosnia, and Turkey. This is in contrast to another widespread species, *T. recurvata,* that I recognize by a less parallel arrangement to the leaves with a sharper contrast in color between the leaf surfaces—notably yellowish green on the abaxial surface and dark green on the adaxial surface, and by cones developing on branchlets that continue their growth. Both have many naturally occurring varieties based on differences in leaf arrangement, leaf texture and branching, and leaf anatomical differences.

Intermediates include specimens similar to *T. contorta* in the W Himalayas. Examples are characterized by long linear ±distichously arranged leaves that in relative thickness to width (as seen in T-section) are similar to either the W Himalayan *T. contorta* (1.5-2.0 mm wide, < 0.5 mm thick, e.g. *Biol. Inst. Dubrovnik* from Bosnia, *Barabas* from Romania, *Davis 13667* from Turkey), or to the E Asian *T. biternata* Spjut (2.0-2.5 mm wide, 0.25-0.33 mm thick, e.g., *Petrak* from Czech Republic, *Moniz* from Madeira, *Handel-Mazzetti* from Greece, *Anderson 42* from Bulgaria, *Davis & Hedge 32208* from Turkey). The W Himalayan *T. contorta* is distinguished from most Euro-Mediterranean *T. baccata* by the presence of dark red, or sometimes yellowish, parenchyma cells (idioblasts) in the leaf spongy mesophyll (in herbarium specimens); however, European specimens occasionally have idioblasts in the leaf mesophyll. In fresh specimens, the intermediates would probably be difficult to distinguish. Of further significance is that the abaxial leaf midrib of *T. contorta* is always papillose (Kvaček 1984), whereas in *T. baccata*, the abaxial midrib varies from smooth to papillose.

I suggest that ancestral *T. contorta* entered the Himalayas from the north during the Miocene uplift (Krishnan 1974), or earlier (Najman & Garzanti 2000), before it arrived in Europe (Frederiksen 1995). Its leaves would likely have lost stomata in adapting to the rising Himalayas where environmental selection would also likely favor the development of papillae on the abaxial leaf midrib (von Frimmel 1911).

As glaciers advanced during the early Pleistocene (2.5–1 mya), the cooling temperatures may have led ancestral *T. contorta* to also retreat into Europe where it then allegedly hybridized with other species of *Taxus* that may have flourished in a subtropical evergreen laurel-conifer forest (Axelrod 1975; Klaus 1989; Kvaček 1984; Mai 1989; Palamarev 1989), but may have found refuge in ravines and coastal areas. Similar patterns of evolution have been suggested for European species of *Abies* (Fady et al. 1992). The significance of numerous European refugia for conifers was suggested by Fady-Welterlen (2005) to account for their "significantly higher" "within species diversity" "than that of other conifer species worldwide." In this regard, it is interesting to note that the association of *Taxus* with "ancient forests" on limestone cliffs in Iowa and in Europe is partly attributed to the topography of the habitat that offers protection from *Homo sapiens* (Larson et al. 2000), whereas a severe decline in European *Taxus* is generally recognized (Heinze 2004).

Taxus engelhardtii Kvaček, described from a late Oligocene deposit in "NW Bohemia," was associated with a mixed mesophytic forest with prevailing broad-leaved componets (Kvaček 1984; Kvaček & Walther 1998) that included *Laurophyllum* (4 spp.), *Cercidiphyllum, Liriodendron, Acer, Ostrya, Betula, Craigia* and other genera. Its leaf shape and arrangement is much like *T. mairei* in Sichuan, Yunnan (Fig. 10) and Guangdong where similar forest types still occur today. Vegetation in these areas—characterized by a distinct dry season—includes species of *Cercidiphyllum* and *Liriodendron* (Hou 1983) that have since become extinct in Europe. In Vietnam, the closely related *T. celebica* occurs in a laurophyll oak forest from 1000–1600 m in elevation in association with *Cinnamomum obtusifolium* Roxb. ex Nees, *Michelia foveolata* Merr. ex Dandy, *M. mediocris* Dandy, *Castanopsis fissa* (Champion ex Benth.) Rehder & E. H. Wilson, *Quercus bambusifolia* Hance and others (Dung 1996; Schmid 1974.). Extant yews in Europe, however, bear little resemblance to *T. engelhardtii*; therefore, it may not have contributed to hybrid complexes that are now apparent in Europe. Rather it may have simply been extirpated from the Euro-Mediterranean Region due to changes in the climate.

However, another European complex appears to have been derived in part from the Irish yew (*T. fastigiata* Lindley), a possible relict of a former subtropical forest. Known initially from two trees in Ireland—that were transplanted at the time of discovery (~1770; Veitch et al. 1881), it has always been regarded a distinct yew even though taxonomists have included it under *T. baccata* (Loudon 1844; den Ouden & Boom 1965). Its linear dark green leaves that are spirally arranged in whorls seem less evolved. Moreover, such radial phyllotaxy is infrequent among yews—occurring at disjunct locations in the Old World, particularly coastal regions—in Spain, Morocco, British Isles, Honshu, Hokkaido, and Sakhalin. Leaves of the Irish yew in cultivated specimens from widely scattered locations were found to be remarkably similar in lacking papillae along 6–15 cells across an abaxial marginal zone and on the midrib as well; these specimens, which are not included in the Appendix, are from Australia (*Boorman,* New South Wales, A), North America (*Spjut s.n.* Oregon, California, Maryland, wba), and Europe (*Baker,* Yorkshire, BM; *Stewart* Hort., Florence Court, Ireland, K; *Baenitz,* Lusitania, S). Perhaps European yews during the Tertiary were more like those now seen in E Asia but have since acquired more papillae on their leaves through introgression with ancestral *T. contorta*, the alleged replacement species. Many yew specimens with dark metallic green foliage from Great Britain appear intermediate between *T. contorta* and *T. fastigiata;* examples are the "Dovaston yew" (*T. baccata* var. *dovastoniana*) and the English yew (in England, *T. recurvata*).

Evolution within the European *T. canadensis* complex is also evident as seen in leaves of one specimen from the former N Yugoslavia (Slovenia, Fig. 5) by the relatively fewer (4–7) stomata rows per band and inflated epidermal cells. Related plants in Madeira, southern France, Norway, and Sweden have more stomata (5–9 rows/band) and less inflated epidermal cells. Characteristics of the Slovenian yew (obtuse leaf apex, 4 stomata rows/band, wedge-shaped epidermal cells) are evident in a fossil leaf from a Pliocene deposit in Bohemia, Czech Republic ("*Taxus* sp. 2," Kvaček 1984).

The increase in cell size and loss of stomata in leaves of the Slovenian yew may reflect adaptation to changes in a climate from a warm temperate humid type with uniform distribution in rainfall towards a climate with more pronounced warmer and drier seasons. The Yugoslavia region is also one of 33 sites in the Euro-Mediterranean region with "Paleomediterranean" woody taxa known from Oligocene, Miocene, and Pliocene deposits (Palamarev 1989). Thus, the Slovenian yew may be a relict of a former Mediterranean montane flora that included the conifer genera *Pinus, Juniperus, Tetraclinus, Abies, Cedrus, Cupressus*, and *Picea* (Palamarev 1989); some of these are reported with this Pliocene yew (Kvaček 1984).

I also distinguish *T. mairei* from *T. sumatrana* by the relatively short inflated epidermal cells on the abaxial midrib (Appendix; Spjut *in adnot.* and on illustrations of packets, A, GH, Jun 1996; Spjut 1998b, 2007). The occurrence of this species in China corresponds mostly to the "*broad-leaved evergreen forests of the subtropical zone*" of Hou (1983) with a climate marked by "distinct dry seasons"—"on mountains below 1100 m in the eastern humid subtropics, or on mountains between 1500 and 3000 m in the western subtropics of the Yunnan Highland" (Hou 1983). Similarly, *T. brevifolia*, a species confined to the North American Mediterranean climate, has wider and taller marginal epidermal cells and fewer stomata (Fig 1B), compared to its putative ancestor, *T. globosa* (Spjut 1998a, 1998b) that has evidently survived in the montane cloud forests of Mexico and Central America. The evolution towards larger epidermal leaf cells has also been noted between fossils and living species of *Amentotaxus* (Ferguson 1978).

The variation in leaf anatomical data for *Taxus* in SW China is also related to the convergence of different floras in that region (Bartholomew 1999; X-w. Li & J. Li 1997; Zhengyi & Sugong 1998). These include the "Turkmenian" in W Himalaya, Tibetan or "Indo-Chinese", Malayan, and Sino-Japanese (Mani 1974; Rao 1974; Rau 1974). In the W Himalayas *Taxus* is represented by the neoendemic *T. contorta*, usually with 7–8 stomata rows per band, and in the eastern region by the paleoendemic *Wallichiana* Group with 15–18 (-21) stomata rows. The relatively lower numbers for stomata rows in *T. wallichiana* (11–15) and higher numbers for *T. contorta* (9–11)—where these taxa overlap in their distribution—is undoubtedly due to hybridization and introgression (Fig. 2C). Further evidence for hybridization involving *T. contorta* is seen in the wider marginal region of cells along the abaxial surface of leaves (MC, Appendix) and the wider angle of leaf divergence from twigs in plants from Nepal and Bhutan (Spjut 2006).

The wide range in leaf anatomical traits for yews of SW China (Fig. 2C, 3B) is also a product of a long evolutionary history of tropical and temperate vegetation types with possibly less extinction of taxa during glacial climates (Hsü 1983), in comparison to greater glacial devastation to the floras of North America and Europe. The oscillating wet and dry periods during the Pleistocene may have led to many new combinations in *Taxus* between anatomical and gross morphological features that were once distinctly correlated with eco-geographic differences prior to the Pleistocene. Introgression of character traits has been correlated with data on the advance and retreat of glaciers for other conifers—such as between *Picea rubens* Sargent and *P. mariana* (Mill.) B.S.P. (Bobola et al., 1996), between *Picea glauca* (Moench) Voss and *P. engelmannii* Parry *ex* Engelm. (Wilkinson et al., 1971), among species of *Pinus* (Axelrod, 1986), and among species of *Abies* (Fady et al. 1992).

The slow evolutionary rate that I have suggested for yew is perhaps not all that surprising in view of its ability to survive almost indefinitely. Individual yew trunks can live several thousand years or more (Loudon 1844; Larson et al. 2000; Thomas & Polwart 2003), and when they fall, the plant still survives by adventitious shoots, or by layering (Hageneder 2007; Loudon 1844); thus, it may continue to survive until perhaps a change in climate forces it to either adapt or perish. Prager et al. (1976) calculated a rate of change in the amino acid sequence for Pinaceae to occur once in every 7.5 my. In *Taxus* this may be longer. By extrapolation from data in Figs. 2, and from paleoclimatic changes earlier discussed, one may hypothesize that one row of stomata may become lost permanently in the *Taxus* leaf as it adapts to slight changes in climate over a period of 10 my during which time it may also spread a distance of some 3000 km (at the rate of 300 km/my).

APPENDIX

Data for all herbarium specimens studied according to continental and political regions and taxonomy.

	SR	MC
NORTH AMERICA		
Wallichiana Group		
Taxus globosa var. globosa		
EL SALVADOR		
Tucker 1073 (US). 2670 m	10	5
HONDURAS		
Armour & Chable 6083 (US). Cerro Sta. Barbara, 2750 m	11	4
MEXICO		
Phyton Oaxaca	11	4
Phyton Oaxaca	10	4
Meisner (K). Veracruz to Orizaba	10	3
	SR	MC
Sharp 52112 (GH). Tamaulipas: El Cielo to Ojo de los Indios	10	3
Pringle (US). Trinidad Iron Works	9	4
Harteg 438 (BM). Hildalgo: Real Monte	9	4
Ehrenberg 1837 (K: **type**). Hidalgo: Real Monte, C. Nabajas	9	3
Taxus globosa* var. *floridana		
Hernandez 01459 (BM). Veracruz	9	6
Meyer & Rogers 2746 (BM). Nuevo Leon/Tamaulipas: 1690 m	7	2
Mueller 1337 (PH). Nuevo Leon: Sierra Madre Oriental	7	2
Mueller 1337 (BM)	7	2

	SR	MC
U.S.A. Florida		
Mohr (PH). Near Bristol	8	6
*Croom*1833. (K: **type**).Near Aspalaga	5–7	7
Ex Canby Herb. (PH). Rock Bluff	7	5
Blanton 7050 (PH). Rock bluff	7	5
Wherry (PH). Rock bluff	7	9
Phyton. Florida.	7	8
Taxus brevifolia		
California		
Hansen 1682 (US). *Sequoia gigantea* Region	8/9	4
Lemmon 1874 (US). Yosemite	7	2
Lemmon 1874 (US). Yosemite	6/7	2
Sudworth 1899. (US). Stanislaus Forest	7	4
Bolander 186 (US). Forest Hills, Devil Canyon	6	–
Leeberg 5054 (US). Lovelock, 3500 ft.	7	2
Stokes (US). San Mateo Co.	6	2
Heller 5941 (US). Lake Co.	5–7	5
Clark (US). Mendocino Co.	6	5
Yager & Bozovsky (wba). Del Norte Co.: Oregon Mt. Rd., 200 m, 3 trees:		
(1) top branch	5	–
(1) middle branch	5	–
(1) bottom branch	5	–
(2) lower branch	6–7	–
(2) middle branch	6–7	–
(2) top branch	5–7	–
(3) lower branch	7–9	–

	SR	MC
Rose 55089 (US). Trinity Co., Buckhorn Summit, 2600 ft	6/7	–
Spjut 12307 (wba). Salmon Mts., 2000 m	6–8	7
Spjut 12307 (wba). Salmon Mts., 1500 m	5	8
Spjut 10171 (wba). Marble Mts., 2000 m	5	–
Dudley (US). Salmon Mts., Foxtail Ridge	5–6	–
Benson 2228 (US). Shasta Co., Hatchet Creek	5	0
Grant 1281 (US). Shasta Co., Dunsmiur	6	5
Oregon		
Fisher (US). Portland	7	–
Collector, no.? (US). Jackson Co.: Wimer	6/7	2
Walpole 153 (US). Jackson Co.: Ashland	6/7	–
Coville (US). Imnaha Natl. For., Billy Meadows	6	4
USFS (wba). Josephine Co.: above Taylor Creek, Minnow Creek Rd., 650 m		
4 specimens from nearby sites:		
(1)	5	–
(2)	6	–
(3)	4–5	–
(4)	6–7	–
Lankford (wba). Clackamas Co., 1060 m	5–6	–
Lankford (wba). Clackamas Co., 930 m	5	–
Lyall 1860 (K). Columbia River	5	–
Nuttall (K: **type**). Columbia River	5	–
Spjut 12301 (wba). E Cascades E of Portland	4–6	10
Beattie 5046 (US). Josephine Co.: 2270 ft	4–6	–
Cusick 3405 (US). Eastern Oregon	4	3
Washington		
Spjut 12302 (wba). E Cascades E of Seattle	6–7	10–11
Horner (US). Blue Mts.	6	–
Meyer 1589 (US). Thurston Co., Mud Bay	5–6	6
Grant s. n. (US). Cascade Mt.	6	–
Cantwell (US). Orcas Island	4/5	–
Fosberg (US) King. Co., Stevens Pass	4/5	–
Idaho		
Cronquist 6187 (US). 20 mi W of Riggins, French Creek	5/6	–
Shields (wba). Idaho Co.: Allison Creek, 3400 ft.	5	–
Cochrane (wba). Idaho Co.: Nez Perce Natl. For., 5600 ft., 2 plants	6	–
	5	–
Montana		
Donner (wba) Flathead Natl. For., nr. Columbia Falls, 3800 ft.		
middle branch	7	–
Donner (wba)	7	–
Donner (wba)	4–6	–
P. C. Standley 18251 (US). Glacier Natl. Park, 1400–19850 m	5/6	–
Thomas 11031 (US). Lake Co.: 8 mi from Polson, 3850 ft.	5	4
Steven Wirt 100 (MRC, wba). Flathead Co.: shrubs	5–6	–
Steven Wirt 100 (MRC, wba)	5	–
Steven Wirt 100 (MRC, wba)	4–5	–
CANADA British Columbia		
MacMillan (PH). Selkirk, 4300 ft.	6/7	–
Calder & Saville 9982 (US). SE of Nakusp	7	–
Macoun (US). Rocky Mts., Silver City	6	6
Macoun 2340 (US). Vancouver Is., Victoria	6	–

Baccata Group
Taxus canadensis

	SR	MC
U.S.A.		
Herb. C. W. Minott (US). Ma: Amherst	7/8	–
Bovin & Blain 753 (PH). Me: Cumberland Co., 425 m	6/7	–
True 164 (PH). Me: Ovis Island, Long Cone	6/7	–
Gilbert 831 (PH). Ky: Carter Co., Cascade Caverns	6/7	–
Allard 12060 (US). Wv: 900–1200 m	6/6	–
Women's College *of Baltimore* (US)	6	12
Palmer & King 205 (US). Va	6	–
Taylor 424 (US). Pa: Bucks Co., Kintersville	6	–
Eames 3432 (US). Ny: Coy Glen, Ithaca	6	–
Spjut (wba) Ny: Ithaca	6	–
Spjut 11778 (wba) Nh:White Mts. Natl. For., Wildriver, 300 m	6	–
Stevenson (US). Vt: Willoughby Lake	5/6	12
Weatherby 5977 (US). Ct: Boston Hollow	6	11
Sheldon (US). Mn: Towers St. Laus	6	12
Fellows 5686 (US). Me: Rockport	6	12
Spjut 12179 (wba). Ohio: Secrest Arboretum	5/6	–
Shreeve 1971 (US). Md: Garrett Co., Bailing Spring	5/6	–
Travis 119 (PH). Me: Cumberland Co.	4–6	–
CANADA: Ontario		
McDonald 223 (US). Ontario: Sagastaweeki Is.	5/6	12
Rouleau 2700 (US). Humber Dist., Twin Lakes	7/7	–
Quebec		
Tae hé & Lepage 332 (PH). Dartmouth River	7/8	–
Asselin 7212. (US). St.-Charles	7/7	–
Pennell 16734 (PH). La Belle Co.	6/7	–
Bartram & Long 649 (PH). Rimousk Co.	6/7	–
Fernald et al. 2404 (US). Gaspé Co., Mt. St. Pierre	6	15
Louis-Alphonse 3547 (US). Baie Missisquo	6	18
Lucien 743 (PH). Laurentides, Bellerive	6/6	–
Louis-Maire 686308 (PH). Mé gantic	5/6	–
Bovin 1268 (US). St.-Catherine	5/6	–
Chas Mohr (US). Montreal	4/5	–
New Brunswick		
Malte & Watson (S: C-2153).	6/7	12–13
Allen 2528 (PH). St. John	5/6	–
Nova Scotia		
Gorham 45139 (US). Halifax Co.: near Halifax, St. Margaret's Bay	7/7	–
Bean et al. 19634 (PH). Yarmouth Co.	7	–
19015 (S: C-2155).	6	19
(S: C-2156). Victoria Co.	6/6	12
Pease & Long 19633 (PH). Cumberland Co.	5/6	–
Bissell et al. 19632 (PH). Digby Co.	5/5	–

	SR	MC
Newfoundland		
Fernald et al. 6738 (PH). Prince Edward Is.	8/9	–
Palmer 1300 (US). Bay Is.	8/9	–
Palmer 1327 (US). Hermitage Bay, Balena	7/7	–
Buochan (S: C-2130).	7/7	18
Rouleau 6545 (US): St. Barbe Distr., E BluePond	7/7	15
*Banks*1766 (BM). Croque	7/7	–
Fernald et al. 26201 (PH). NW Coast	6/7	–
Robinson & Shrenk (US). St. John's	6/7	–
Rouleau 5533 (US). Gander River	5–7	–
Fernald & Wiegand 4414 (PH). Valley of Exploits River	6/6	–
Fernald & Long 27305 (PH). Pistolet Bay	6/6	–
Wiegland & Gilbert 27304 (PH). Highlands of St. John	5/5	–

EURO-MEDITERRANEAN

Baccata Group

Specimens ranked first by number of stomata rows then by marginal cells for ***Baccata* Alliance,** *T. canadensis* noted separately under each country.

	SR	MC
ALGERIA		
Swingle (NA). Chria near Blida	12	4
Reichenbach (K). Atlas, Blida	9	4
Gamble (K). Atlas des Demia	8	4
Olaptin (S: C-2070), Atlas, Blida.	7/8	4
Davis 52628 (BM). Cedrus forest, 1900–1950 m	9	6–7
Univ. Algeria Apr 1912 (NA).Atlas, Blida	9	6
MOROCCO		
Trethewy 85 (K), *pendula*. Ifrane 1400 m	10	6
Lewalle 8670 (BM). Ifrane 1400 m	10	4
Lewalle 8670 (BM).	8	–
Lewalle 9670 (BM). Ifrane 1400 m	9	6
Davis 49209 (BM). Ifrane 1700 m	9	5
Lynes (BM). Mid Atlas, Azrou, 5700 ft	9	6
Haout 938 (BM)	9	5
***Davis 55121* (BM). Ifrane, Cascada, 1580 m**	**9**	**8**

Taxus canadensis

	SR	MC
Font Quer 1928 (BM).Kaloa to Tauka, 1500 m	8	7–9
PORTUGAL		
Goncalves 4625 (BM). Azores	12	4
Yoller 61 (BM). Sierra Jerez [Spain]?	12	3–5
Goncalves 4491 (BM). Azores	10	4
ex Herb. Moniz (K). Madeira	10	4
Cyrén (S: C-2058). Ser. Estrela	10	6
Fontee et al. (S: C-2047). Ser. Estrela, 1400 m	10	5
Fontee et al. (S: C-2047–2). Ser. Estrela,	9	5
Meaden 1865 (K). Madeira	9	4
Moller (BM). Serra Gerez: Vidoal	8	4

Taxus canadensis

	SR	MC
Lowe 570 (BM, bottom specimen). Madeira	11	7–14
Lowe with 570 (BM, top specimen)	8	10
Lowe ex Barby (US). Madeira	7	12
SPAIN		
H. Elias 4353 (BM). Burgos: Ser. Obarenes, 1000 m	11	5–8
Modesto Laza Palacios (K). Ser. Tejeda & Almijara, Malacitana Prov.	10	4
no data 1878 (US). Laguna	10	4
Sennen 7087 (BM). Barcelona	10	5
Roivainen (S: C-2075). Guipúzcoa, 900 m	10	5
Sandwith 4452 (BM), Huesca: Ser. Guara	9	4
Heywood & Davis 490 (BM). Ser. Cazoria: Yedra	9	4
Rodriquez (K). Serrania buenia	9	8–11
Bianor-Maire (BM). Baleares, 1600 m	9	5–9
FRANCE		
Fosberg 41055 (US). Jura Mts.	10	4
Endress Aug 1831 (K). Pyrenees	10	6
Endress Aug 1831 (S). Pyrenees	8	5
ex Herb Comby (PH)	9	4
Tidestrom 12814 (US)	9	4
Massonnet (K). Pyrenees	9	5
Herb. Hook., 1867 (K). Pyrenees	8	4
Herb. Churchillanum (K). Corsica	7	–
C. Lagerheim & G. Sjogren Jul 1844 (K). Batsmanshus Paroeciae Elfkarl by Rosalagiae abundans	8/9	5

Taxus canadensis

	SR	MC
Herb. Gombault (S). Sainte Baume	9	18
UNITED KINGDOM		
Gamble 19866 (K). Berkshire Dist	11	4
Bowden & Hillman 433 (BM, globose epidermal cells). Nottinghamshire	**11**	**3–5**
Gamble 28894 (K). Weltham woods [England SW]	11	5
Albarnes 26 (K). Dorsey: churchyard [England SW], 350 ft	10–11	8
Michaelstone (K). British Isles, England	10	4
Turrill 4903 (K). Leicestershire, Charwood Forest	9/10	4
Ap. ys 77–390 (K). Kent	10	4
Turrill (K). Surrey, Box Hill [England SE]	10	4
Fraser (K). Surrey, Box H ill	10	4
Fraser (K). Surrey, Chalk Pits	10	4
Bean & Hill (K). Scotland: Neopath Castle, Tweedsdale near Peebles	10	4
Ball 1838 (US). Surrey, Jumper Hill	10	4–5
Ex. Herb. Bidwell (BM), *dovastonianum*. Westfelton	10	4
Ex. Herb. Gordon (K), *dovatsonianum*. Westfelton.	10	4
Jackson (BM). Westfelton (Dovaston yew, original)	10	5
Lewis 721 (BM). Monmouthshire	10	5
Jarrell (K). Kent: Shorehane	10	5
Bennett & Croydon 713 (US). Riddlesdown	10	5–6

	SR	MC
Hooker (PH). Kent	9	3
Barron (K). Kent, Buckland	9	4
? (K). Kent, "var. *washingtonianum*"	9	4
Valpy (K). Elsing, Norfolk	9	4
Boswell (BM). Shropshire, Lyth Hill	9	4
Brubaker 1960 (PH). Druids Grove	9	4
Roper 1525 (K). Bristol, Birdhamdown	9	4
Carruthers (K). Ireland: Pollawaddy	9	4
Aug. 1874 (BM). Perth Co.? [filed under Portugal]	9	5
Turrill (K). Yorkshire: 3 mi. from Richmond	8	4
Hubbard (K). Sussex: Bury Hill	8	4
Jackson (BM). Highclere, Saddam	8	4
Turrill (K). Scotland: Loch Lomond	8	4–7

Taxus canadensis var. *adpressa*

	SR	MC
***Summerhayes 2581 (K).* E Kent**	**8**	**4–6**
SWITZERLAND		
Kellermann (US: 518500)	10	3
Herb. A. Gray (K)	9	5
Fr. Castella (US). Le Pissot sur alboue, 1000 m	7	6–7
GERMANY		
Reichenbach fil. (PH). Dresden	11	3
Martius 1831 (PH). Bavaria	9–11	4–6
Martius 1831 (K).	9/10	4
Milchbuder (K). Bavaria	10	4
Petzi 1444 (K).Bavaria	8/9	5
Reichenbach, ex Short Herb. (PH). Dresden	7–8	4
Keller (PH). Darmstadt	7	4
Martius 1831 (K). Bavaria Alps	7	4
POLAND		
Baenitz (US). Silesia: Proskau, 180 m, "*f. dovastonii*"	10	6
Baenitz (US) *epacroides*. Silesia: Breslau, 120 m, "v. *recurvata*"	9	4
Baenitz (US). Silesia: Breslau, 120 m, "f. *epacroides*"	10	4–5
Baenitz (US), *epacroides*. Silesiaca: Breslau, Scheitniger Park 120 m	8	4
Baenitz (US). Silesia: Breslau, 120 m, "f. *erecta*"	9	9–10
CZECH REPUBLIC		
Jirasek & Suza (K). Moravia Centr.: 4–450 m	10	4–6
Jirasek & Suza (US). Moravia Centr.: 4–450 m	10	5–6
Petrakm, Fl. Boeh. & Morav. exsic. 99 (BM)	8	4–5
AUSTRIA		
Ex Pickler Herb. 1895 (US).	11	4
Ex Herb. Pichler (US: 347988, lower specimen). Tirol	10	4
Ex Herb. Pichler (US: 347988).Tirol	8	4
Ex Shulte Herb. 1863 (K)	10	4
Hayer (S: C-2034). Salzburg	10	6
Gander 1869 (K). Tirol	9	6
Gander 1869 (US: 157025). Tirol	9	6
Keck (US)	9	5

Taxus canadensis

	SR	MC
A. Hayek & F. Hayek (BM). Styria superior: Kulmburg	9	17
HUNGARY		
Herb. Láng (PH)	10	4
Schönach 3084 (S: C-2061A)	10	4
Schönach 3084, Austr-Hungar. (US). 445 m	8	3
Wagriesh (US: 451917). Vorarlbergia, 445 m	8	3
Wagriesh (US: 481917). Dolüa	8	3
Boros (BM). Comit. Boraod. Ohassa, 550 m	9	5
Lémke (S: C-2042). Bakony: Mikl¢spalhazy	9	4–5
Schönach, Aust.-Hungar. (US: 966290), *epacroides* 445 m	8	4–5
Ex Herb. Mus. Nat. Hungar. (S: C-2041), Bakony	8	4
Schönach 3084, (BM). 445 m	9	6

Taxus canadensis

	SR	MC
Schönach 3084 (S: C-2061 R Specimen). 445 m	5–6	19
ROMANIA		
***Topa, Bot. Mus. Exsic.* (US). Bucovina: 400 m**	**12**	**16**
Topa, Bot. Mus. Exsic. (S: C-2024). Bucovina, 400 m	10	3–5
Topa, Bot. Mus. Exsic. (US). Bucovina, 400 m 9	4	
Anderson 102 (K). Balkan Exped., Cajan Pass	9	4
Mititleu & Barabas (BM). Bucovina: Darmanesti, 500 m	8	5
BULGARIA		
Kotschy (P)	8	4
Anderson 42 (K). Sofia: Vitorha	9	4
ITALY		
Herb. Hook. 1814 (K). Montagnes	10	3/4
Levier (BM). Florentino	10	4
Lenander 1933 (S: C-2008). Lago di Garda, Riva, Sydtyrolen	10	4
McDonald: I-37 (US). Cult.	10	5
McDonald: I-37 (PH). Cult.	8	5
Solla (US: 280040).	9	3–4
Baroncini 16 Sep 1893 (US)8/9	5	
Fireuze (BH). Cult.	10	9
Martelli (PH). "Iter Sardoum", Limabara [Sardinia]	8/9	10
[YUGOSLAVIA]		
***Biol. Inst. Dubrovnik 37* (NA). Bosnia: Mt. Trebevic near Sarajevo, 1450 m**	**12/13**	**3–4**
Kosarim (S: C-2065), Macedonia, Petiska	10	5
Baldacci 169 (K). Albania	8/9	5
Rohleana 1908 (BM: 17197). Montenegro	7/8	4–5
Curic 1897 (K). Bosnia	8	9
Biol. Inst. Dubrovnik 136 (NA). Bosnia. Mt. Plasma near Jablanica, 1500 m	6/7	2–4
Woloszczak (K), Tatra	9	6–9

Taxus canadensis

	SR	MC
***Berglund* (S: C-2066; var. *adpressa*). Slovenien: Bled, berget Straza**	**4–6**	**24**
GREECE		
Georginda & Tzanoudakis 631 (BM). Artis: Mt. Tzoumarka	10	6
HGT 884 (K). Hills N of Xant Is	9	4

	SR	MC
Heldreich (S: C-2023). Oeta, 4500–6000 ft.	9	2–4
Greola (PH). "Mts. of Tyrah"	9	4
Guiol 2260 (BM). Mt. Olympus	7/8	3–4
Handel Mazzetti (K). Mt. Olympus, 750–850 m	8–9	8

TURKEY

	SR	MC
Balonsa (BM). Taurus	9	5
Balonsa (P). Taurus	8	5
Davis & Hedge 32208 (BM). Coruh, Savval Tepe above Murgul, 1400 m	7	6
Sintensis 5118 1892 (P) Paphalogonia: Wilajet Kastanbuli	9	8
Sintensis 5118 (K)	7	8
Murray 936 (NA). Between Molla Veyis and Meyden, S of Ardesen, 750 m	8	–
Davis 13667 (K). VA. Jenigli (Caira [Caria ?]) (Denizli, Boz Da, *Davis 13447*), 5000–5500 ft	8	8–10

IRAN

	SR	MC
Koelz 16208 (US, distinct for obconical to 4-lobate seeds). Gozlu, Mazandaran	8–9	7–10

SYRIA

	SR	MC
Haradjían (K). Dúldúl: Mt. Amanos, 5000–7000 ft	10	4
Haradjían 2341 (S). Dúldúl: Mt. Amanos, 5000–7000 ft	8	4
Gesbeldagh (BM)	9	4
Gesbeldagh (US)	10	4
Haradjían 3865 (S). Dúldúl: Mt. Amanos, 1500–2000 m	10	8–10
Delbés (P). 1000 m	9	8

RUSSIAN REGION

Estonia

Taxus canadensis

	SR	MC
Lundström 742 (S). Eosl near Karriland	9	16
Lundström 579 (S). Ösel, Sworbe	9	22
Lundström 562 (S). Ösel, Sworbe	7	15

Transcaucasia (Caucasus Mts.)

	SR	MC
***Elias et al. 5615* (NA) Ukraine Crimea, 1150 m**	**9**	**9**
***Princeps Kascelsky, ex. Herb. Hort. Imper. Petro.* (S). Caucayas Hosharia**	**15**	**6–7**
***Busch* (K). Caucasus, Terek**	**11**	**12–14**
***Woronowa* (S: C-2027). W Transcaucasia: Suchum, Petkir (Fl. Madshara)**	**13**	**1**
Dmitrieva (NA). SW Georgia, Black Sea near NE Turkey, Adzharia, 900 m	11	4
Inst. Bot. Acad. Sci. Armenia (US). 22 Mar 1946	10	4
Szovich 610 (S: C-2072). Armenia: Tschunakuchi	10	4
Szovich 610 (P). Armenia: Tschunakuchi	9	4
Ex. Herb. Inst.. Bot. Ac. Sc. URSS (US: 2560106). [Transcaucasia]	9	4
In Russian #75 (P). Azerbaijan [Kura Mts.]	9	8
Herb. Komaróv (US: 1862552). Armenia	7/8	6
***Prilipko* (K). Transcaucasia**	**9**	**10**
Goghika (NA). Caucasas: Azerbaijan, Chanlar, 1800 m	10	8
***Brzhezitzky & Kasumov H196* (US). Azerbaijan**	**10**	**15**

Taxus canadensis

	SR	MC
Kousnetzoff 89 (US: 254512). [Russian Federation] Kuban	10	18

NORWAY

	SR	MC
Gamble 28933 (K). West Dalen	10	4

Taxus canadensis

	SR	MC
Anderson (US: 1091452). Kolsås	5	18

DENMARK

	SR	MC
Herb. Joh. Lange 1866 (K)	10/11	–
Herb. Joh. Lange 1866 (K: Right specimen)	8	4

SWEDEN

	SR	MC
Thedenius (PH), Göteborg	9–10	4
Thedenius (US)	8	4–6
Steinvall 1872 (K). Södermanland	10	6
Henriksson (K). Dalsland:Gunnarans	8/9	6
Holmgren (US: 1276222). Blekinge	8	5
Lindberg 419 (K). Ekerö	11	8
Herb. Bot. Berjianus (S: C-2177), *"washingtonianum"*	10	8
Bjornstrorn, ex Mus. Stockholm (US). Podermanlane? [Södermanland]	10/11	10

Taxus canadensis

	SR	MC
Asplund (US: long-needled specimen). Södermanland	9	20
Asplund (US: short-needled specimen).	8	22

FINLAND

	SR	MC
Florström (BM). Alandia: Lemland	11/12	4
Florström 1909 (K)	10	3–6
Vidlund, Helsinki Exsic. (K). Lemland	8	4

EAST TEMPERATE ASIA

Cuspidata Alliance

RUSSIAN FEDERATION

Taxus biternata

	SR	MC
B. Cerereu (A). Far East Region: Pryanyk For. Div.	11	12

***Taxus umbraculifera* Complex**

	SR	MC
Kypehisnova (A). Primorye Prov.	14	–
Kypehinova (A) Primorye Prov., Bay of Peter, First Sea Reserve, Is. Stenin	10	5
Dvorakovskia & Bokina (A). Sakhalin Is.	11	8
Palczevsky 3601 (K). Primorye Prov.: vicinity of Vladivostok	11	8
Palczevsky 3601 (US)	9	–
Palczevsky 3601 (A)	8	–
Lyubarsky 2 (A). South, Sikhote-Alin, foothills, Mt. Hezalaza, River Beryozovoy	8	7
Esus 203 (K). Sakhalin Is.	8	12–15

MANCHURIA

Taxus biternata

	SR	MC
Ex herb. hort. bot. Petro. 1860, Maximowicz (P). Mandshuria SE	10	6

	SR	MC
Skvortzov 20 Sep 1931 (A). N Manchuria, Sochintzest, forest, tree	10–11	8
In Russian No. 75 (P). Jilin (Kirin)	9	8
C. H. Chen 539 (A). Jilin (Kirin)	8	6
Maack 1855. (GH: top specimen)	7	7
Purdom (GH). N China [Shaanxi: Tai-pei-shan *fide* Rehder & Wilson in Sargent 1914]	7	13
T. umbraculifera Complex		
Palczevski [Komaróv] 88 (K). Manchuria: Rossica	14	14
Palczevski [Komaróv] 88 (BM)	12	9
Maack 1855. (P)	11	8
Ex herb. hort. bot Petro.1860 (Bunge), Maximowicz (P). Mandshuria SE	12	10
Ex herb. hort. bot. Petro. 1860, Maximowicz (S) Mandshuria SE	12	8
Ex herb. hort. l.c. (P)	10	8
Ex herb. l.c.(GH)	7	–
G. Fenzel (A). Schenhsi merid., Taipei-schan	7	13

KOREA

Taxus biternata

	SR	MC
Wilson 10519 (US). Kyongsan, Nemon-rei	13	15
Wilson 10519 (A)	10	14
Wilson 9484 (A), Hallai-san down to Mushroom House, bush	12	8
Wilson 9097 (A), Shinkabachin Heizanchien to Ehoshin, Kankyo-N Heian divide, tree	11	16
Wilson 8685 (A). N. Heian Prov.: O.G.M. Co. Mines, Pukchin	10–11	12
Wilson 8685 (US)	10–11	12
Wilson 8685 (K)	10	10
Komaróv 1897 (GH). Pen-nian Prov.	10	4–6
Wilson 10688 (US). Kyongsan, Nemon-rei	9–10	6
Wilson 10688 (A)	9	8–9
Wilson 10688 (K)	7	6

Taxus umbraculifera Complex

	SR	MC
Wilson 8538 (US). Oagelet Island, 0–900 m, bush	12	12
Wilson 8538 (A)	12	12
Wilson 9332 (A). Kyongsan Prov.: Nemon-rei, tree	12	10
Faurie 1512 (BM)	9/10	9

JAPAN

Taxus cuspidata

	SR	MC
Ex Herb. Zuccarini (M: **type,** *T. cuspidata*) Japan	11–12	24
Ex Herb. Zuccarini (K: **type,** *T. cuspidata*) Japan	11–12	18
Jack (A). Hokkaido: Sapporo	12	20
Jack (GH). Hokkaido: Sapporo	10–11	16

Taxus biternata

	SR	MC
Makino 43775 (S), Tokyo Pref.: Oizuni, Nepymawku	16	12
*Mujabe*1884 (A). Hokkaido: Ishikasi	14	14
Makino 43779 (S). Chiba Pref.: Mt. Kiyosumi	13	6–8
Uno 2611 (A). Nagano-ken, Okmachi	13	9
Mochizuki (A). Mt. Nantai, Lake Chuzenji	12	10
Wilson 7544 (A). Kai prov., Nakaihinsen, 1200 m, hedge	12	9–12
Sargent (A). Hokkaido, Cosl Mines, Utishini	11	10
Arimoto (A). Sapporo, Yezo	11	13
Nitzelius (S: C-2111), Göteborg cult., from Hokkaido: Kamikawa, Yamabe	11	18
Wilson 7778 (A). Hondo, Sernja Prov.: Yamanaka on Fuji-san, tree	11	–
Wilson 7778 (K)	9	14
Hatusima 13858 (A). Kagoshima Pref., Mt. Takahuma, tree	10	–
Ex herb. horti bot. Petropolitani, Maximowicz. 1862 (P), Yokohama	9	6

Taxus umbraculifera Complex
Taxus caespitosa var. *caespitosa*

	SR	MC
Mizushima 1985 (A). Honshu: Mt. Hakkoda	11	13–18
Wilson 7133 (A), Honshu: Hakkoda, 1000–2000 m, shrub	11	8
Ex herb. horti bot. Petropolitani, Maximowicz. 1862 (GH), Yokohama	10	10
Ex herb. horti bot. Petropolitani, Maximowicz. 1862 (P). Yokohama	10	10
Wilson (A). Honshu: Mt. Daisen (**topotype**), 2000 m, shrub	10–11	9
Makino 43792 (S). Honshu: Mt. Daisen (**topotype**)	10/11	10

Taxus caespitosa var. *latifolia*

	SR	MC
Shimotsake 446 1888 (US, anatomy like *T. mairei).*	15	16
Faurie 6345 (K, **isolectotype**)	14–15	12
Faurie 6345 (P, **lectotype**)	11	8
Bataw, Herb. Lugd (P). Honshu: Shimane	14–15	–
Faurie 5114 (P)	13	10
Faurie 5114 (P)	12	6
Makino 43769 (S), Honshu: Akita Pref.	12	7–8
Tomitar ex. Makino 43780 (S), Honshu: Kanagawa, Mt. Imaizumi	11	8
Wilson 7265 (A). Hokkaido: Shiribeshi Prov., 1300–2000 m	11–12	10
Mizushima 401 (A). Honshu: Prov. Kozuke, Oze-ga-hara	9–10	10
Mizushima 1989 (A). Honshu: Mt. Hakkoda	9–10	7
K. Muijabe 17 Sep 1910 (A). Hida, Takayama	9	14
Shimotsake (P). Honshu: Nikko	8	8
Ex herb. horti bot. Petropolitani, Maximowicz. 1862 (P). Yokohama (with *T. biternata*)	11	8
Ex herb. horti bot. Petropolitani, Maximowicz. 1862 (US). Yokohama (top specimen)	10	7
Ex Herb. Zuccarini, 1842, with *ex* Herb. Lugd. Batav. (GH). Japan	8(–11)	12

Taxus umbraculifera

	SR	MC
Ex Herb. Lugd. Batav. (P). Japan	11–14	15

	SR	MC
Suzuki 499003 (A), Honshu: Mt. Ooyhama, Kanagawa-Pr, cult.	14	13
Faurie Dec 1904 (A), [Hokkaido], cult. and in forest	13	13
Muroi 1969 (A). Honshu: Mt. Fujiwara	12–13	14
Wilson, ex. Sakurai (A), Honshu: Kyaraboken, cult. "*nana*"	10	13
Muroi 5933 (A). Honshu: Mt. Himekami	10–12	10
Sapporo Agric. College (PH). Hokkaido: Kitami Prov, Rishiri	11	11
*Sapporo Agric. College*1885 (A). Hokkaido: Niarenai?	9–10	13
*Sapporo Agric. College*1878 (A). Hokkaido	11–13	11
Naito (A), ex. Herb. Kagoshima Univ. Shimane Pref., Mt. Sentsu-zan.	11	8
Hatusima 13858 (A). Kagoshima Pref., Mt. Takahuma, tree	11	8
Shiota 4441 (A). Hondo, Mino Prov., hort.	11	8
Muroi 30 (A), Honshu: Hyogo Pref., Mt. Hyonosen	10	8

Taxus umbraculifera var. *hicksii*

	SR	MC
Muroi 5603 (A). Hyogo Pref.: Kumatugi, Mikata-gun	13	14
Muroi 5424 (A). Mt. Hatibuse	12	8
Muroi 5648 (A). Wakasugi	11–12	10
Muroi 3593 (A). Iwate-Pref.: Asagishi	11–12	10
Muroi 3698 (A). Gifu-Pref.: Takayama	11	10
Muroi 3715 (A). Nagano Pref.: Kamikochi	11	8

ASIA: HIMALAYAS

Baccata Group

AFGHANISTAN-INDIA

Taxus contorta var. *contorta*

	SR	MC
Sprague 730 (K). Murree	6	4–5
Aitchinson (K). Kurrum Valley, 7500–9000 ft	6	4
Sinnott et al. 146 (K). Between Gotchbok and Kubkot Valley, 2750 m	7	3–4
Stewart 15343 (US). Murree, 7000 ft	7	–
ex Herb. Schlagintweit (PH). NW of Srinagar	5	–
Stewart 7374 (PH). Sonamarg, 10,000 ft	6/7	4
Mukinji (K). Lada Valley	6	4
Stewart 8414 (US). Kashmir: Pahlgam	5	4
Stewart 8414 (A). Kashmir: Pahlgam	7	3
Stewart 8414 (PH). Kashmir: Pahlgam	7	3
Stewart 12001B (A). Kashmir: Pahlgam 2600 m	7	6
Schlagintweit (P). Kashmir: Báltal to Númner	7	–
Kenyoer & Dugeon (PH). Bureah, 11,000 ft	7	5
Rau 31770 (A). Garhwal to Lake Hemkund, 3200 m	7	–
ex Herb. Falconer 1000 (S: C-1994). Kumaon, Dwali? 8500 ft	7	4
ex Herb. Falconer 1000 (P). Kumaon	7	5
Koelz 10285 (A). Punjab: Kulu, above Bandrole, 8000 ft	7–8	–
Schlagintweit 8941 (GH). Kashmir: Sukhi across Bamsuru and Chaia Pass to Khdrsali, 9000–15400 ft	7–8	3
Rodin 5313 (US). Punjab Province: Rosenhiem, Murree	8	5
Stewart 5931 (A). Kashmir: Pahlgam, 7000–10,000 ft	8	–
Heybrook 29 (K): Kashmir: Pahlgam 2600 m	8	4
Lace 301 (A). Bashahr, Uri Forest	8	–
Stewart (PH: 829196). Dharmkat, Dharmsala, 6000 (ft?)	8	8
Gamble 23507 (K). Jaunsar Dist., 10,000 ft	8	1–3
Stewart 10663A (PH). Gulwarg, 7000–10,000 ft	9	12
Laig Raus (P). Siwalik and Jaunsar Div., 10,000 ft	9	5
Pengelly (K). Chumba	10	4
Bertoloni (BOLO: **type,** *T. orientalis*). Western Sikkim	10–11	3

NEPAL

Baccata Group

Taxus contorta var. *contorta*

	SR	MC
Stainton et al. 7832 (BM). Chingnon, 10,000 ft	7/8	4
Polunin et al. 1353 (BM). Dhotar, 9600 ft.	9	4
Polunin et al. 432 (BM). Chankeli Range, 8000 ft	11	5
Polunin et al. 5050 (BM). W of Jumla, Belas Gaejigeth, 10000 ft	9	6
Polunin et al. 1873 (BM). Chatlwe, 9000 ft.	10	5
Gardner 557 (BM). Shios Khola, 8500 ft	9/10	5
Stainton et al. 734 (BM). Lete, S of Tukucha, 8000 ft	10	5
Ottba et al. 8311066 (BM). Marayandi Khola	11	0
Mikage et al. 9550282 (BM). Dhaulagiri Zone, 2405 m	10/11	4
Stainton et al. 5616 (BM). Chingnon, N of Tukucha, Gadaki Valley, 10,000 ft	11	7

Taxus contorta var. *mucronata*

	SR	MC
Dobremez 2106 (BM).	8/9	10
Wraber 514 (BM). Hanangi: Karayundi Valley, 3100 m	8/9	10

Sumatrana Group

Taxus sumatrana

	SR	MC
Herb. Banerji, 1953, in adnot. T. bounoniana Carr. (A). E Nepal: Khanigaon to Kalanti, 6,000 ft.	12	16

Wallichiana Group

Taxus wallichiana

	SR	MC
Wallich 6054A (M: **Original Material**). [Nepal]	15	6
Wallich 6054A (K: Duplicate of Original Material). [Nepal]	14	5
Wallich 6054A (K: Duplicate of Original Material). [Nepal]	12	5
Wallich 6054A (S: Duplicate of Original Material). [Nepal]	13–15	2
[Wallich] (GH: Duplicate of Original Material). Napalia.	15	4

	SR	MC
Beer 25316 (BM). Above Sedua, 9400 ft	14	4
Stainton et al. 1398 (BM). Arun Valley, N of Kutiar, 9000 ft	14	4
Stainton et al. 6601 (BM). Eastern: Duon Kosi, Chaunrikarua, 9500 ft	13	4
Stainton et al. 4496 (BM)	13	4
Griffith 2006. 9000–10,000 ft	13	3
Stainton et al. 5102 (BM)	13	4–5
Tabata et al. 10585 (A). Soluhumbu Dist.: Lamujo to Chumawa, 2450 m	12	4
***Tabata et al. 10585* (BM)**	**11**	**0**
Stainton et al. 8296 (BM). Pembrang?, 10,000 ft	11	3
Williams 458 (BM). 9500 ft	10–11	4/5
Ohba et al. 8310264 (BM). Thulo Kobar to Ran Thanti, 2600 m	9–11	4
Ohba et al. 8310264 (BM)	11	4

Taxus phytonii

	SR	MC
Williams 1014 (BM). 9000 ft	16	4

BHUTAN

Baccata Group

Taxus contorta var. *mucronata*

	SR	MC
Ludlow et al. 16035 (A). Eastern, Ha: 27.22′ 89.18′, 9,000 ft	11	9
Ludlow et al. 16035 (BM)	9–10	8

Sumatrana Group

Taxus celebica

	SR	MC
Cooper & Bulley 2833 (BM). Rinchu Timakha, 6000 ft	13	13

Wallichiana Group

Taxus wallichiana

	SR	MC
Ludlow et al. 18672 (BM). Tunle La. near Kinga Rasdah, 11,000 ft	12	2
Ludlow et al. 18672 (A). Tunle La near Kinga Rapden, 11,000 ft	12+	5
Grierson & Long 4417 (A). Thimphu Dist.: summit of Dochong La, 3110 m	12	6
Cooper & Bulley 2600 (BM). 7,500 ft	16	4
Bartholomew & Boufford 3917 (A). Above Motithang, W of Thimphu	10–11	6

NE INDIA & TIBET

Sumatrana Group

Taxus celebica

	SR	MC
Kingdon Ward 19324 (BM). "Assam" [**Tibet**]: Rima, 7000 ft	11	32
Clarke 38308 (K). Khasia: Maophlang	9	32

Taxus kingstonii

	SR	MC
Mann 1885 (K). Khasia Hills, l.c.	13	20
Mann 1885 (BM), l.c.	15	15
Mann 1885 (P). Khasia Hills, l.c.	13	19
Kingdon Ward 18751 (A). Khasi Hills, Mawphlang, 6000 ft	12	15
Hooker 1337 (K). Khasia: 5000 ft	13	16
Hooker & Thomson 1855 (P)	11	12
Hooker & Thomson 1855 (P)	10/11	8–10
Hooker & Thomson 1855 (P with seed)	13	10
Simmons 484 (P). Assam: Khasia	13	12

Taxus sumatrana

	SR	MC
Mann 1885 (A). Khasia Hills: Nunghuai, 5000 ft	24	12

Wallichiana Group

Taxus wallichiana

	SR	MC
Wallich (M: **Lectotype**). Eastern	13	4
Biswas 439 (A). E Himalaya	13	5
Biswas 439 (A). E Himalaya	10–11	5
Kurz (A). Sikkim: Tongloo	13–15	–
Raijada 18919 (A). Cult., Dehra Dun, Bot. Gard. Darjeeling	14	4
Griffith 5002, ex Herb. Griffith. E Himal. (P)	**12**	**0**
Griffith 5002, ex Herb. E India Co (P)	13	4
Griffith 5002, ex Herb. Bunge E Himal. (P)	13	4
Hooker 77 (P). Khasia, 5000–6000 ft	16	4
Hooker 77 (P). Khasia, 5000–6000 ft	16	4
Griffith 2(7)606 Assam (P)	15	4
Kingdon Ward 17271 (A). Sirhoi: 8000 ft	15	4
Kingdon Ward 17271 (BM). Sirhoi: 8000 ft	15	4
Vos et al. 148 (NA). West Bengal: Singalila Range, 8400 ft	15	5
C. B. Clarke 436743 (BM). Khasia: 4500 ft, Vale of rocks	14	4
G. Watt 5955 (A). Manipur: Seriphari, 10,000 ft	15–17	–
G. Watt 5955 (P). Manipur: Seriphari, 10,000 ft	17	4
G. Watt 6493 (P). Manipur: Sirohifarar, 7000 ft	16	4
G. Watt 6208 (P). Manipur: Jakpho, 11,000 ft	18	4

Taxus wallichiana var. *yunnanensis*

	SR	MC
Hooker (K). Sikkim: 7000–10,000 ft	14	3
Hooker (K). Sikkim: 7000–10,000 ft	14	3
Kingdon Ward 18990 (BM). Jakpho Range 7300 ft	14	4
Clarke 41238B (K). Jakpho, Naja Hill	11–12	3
Kingdon Ward 7755 (K). Barail Range, Naga, 9000–10,000 ft	13	4
Kingdon Ward 8090 (K). Assam [**Tibet**]: Chiban, Delei Valley, 6000–7000 ft (K)	14	3
Kingdon Ward 8594 (K). Assam: [**Tibet**] Delei Valley, 9000 ft (K)	15	4

Taxus phytonii

	SR	MC
***Ludlow & Sherriff 3719* (BM). Pachaksihri, Laluma, 94°15, 27°45, 7000 ft**	**12**	**0**

MYANMAR (Burma)

Sumatrana Group (*Taxus kingstonii*)

	SR	MC
Oliver 4 Sep 1894 (K). Bernardmyo, Ruby Mines	15	8
Oliver (K) 14 May 1892, 5600 ft	12	5–6

Wallichiana Group

Taxus obscura (Chinensis Subgroup)

	SR	MC
Oliver (K) Ruby Mines, 6500 ft	13–15	5

Taxus suffnessii (Wallichiana Subgroup)

	SR	MC
Kingdon Ward 21901 (A). West Cental Esakan, 6400 ft	12–15	6
Kingdon Ward 20901 (BM). W Central	18	0
Kingdon Ward 20902 (A: **holotype**) North Triangle, 9000–10,000 ft	12–13	–
Kingdon Ward 20902 (BM, **isotype**)	16	2
Kingdon Ward 13003 (BM). 27°45′N, 97°50′E, 9–10,000 ft	20	0
Hla & Koko (K) Myintkyina: Sumprabum, 8600 ft	15–16	2

Taxus wallichiana* var. *wallichiana

	SR	MC
Kingdon Ward 9214 (BM) Northern, Adung Valley, 97°30–98°30′, 27°30–28°30′, 6000 ft.	17	4
Kingdon Ward 9214 (A)	16	4
Kingdon Ward 9375 (A). N Adung Valley, 97–98°30′ 27–28°30′ 7000– 8000 ft	12–13	4

Taxus wallichiana* var. *yunnanensis

	SR	MC
Kingdon Ward 22819 (BM). Mt. Viatoria, 9000–10,000 ft	16	4
Kernode 17205 (K). Myintkyina: Laikan-Fenshuiling Rd, 8000 ft	12	3

THAILAND

Chinensis Subgroup

Taxus obscura

	SR	MC
Lobb 461 (BM) Malaya	12–14	8

***Sumatrana* Group (*T. sumatrana*)**

	SR	MC
Kerr 20146 (K). Kao Kuading, 1200 m	15	14
Kerr 20146 (BM)	12	14

VIETNAM

Sumatrana Group

Taxus celebica

	SR	MC
Evrard 305 (P). Dalat: ravin buisé an chalet Rimaud	9/10	24
Evrard 1438 (P). Lâm Dông	12	24
Schmind 1960 (P). Dak Tria- Manline, 1400 m	8	32
Schmind 1960 (P). Dalat: Dau Lamghi	9	24
Schmind (P). Dalat: Dak Tria, 1610 m	11	32
*Van Cuong 12891*1960 (P). Dalat: Manline, 1610 m	12	23

Wallichiana Group

Taxus chinensis

	SR	MC
Hiép & Chan 405 (P). Hoa Binh, Mai Chôu, Pà Co, 900–1500 m	13	8–13

Taxus* aff. *chinensis

	SR	MC
Poilane 4150 (P). Phu Khanh: Nha Trang, 1500 m	11	4
Poilane 4150 (A). Nha Trang, 1500 m	10–11	4
***Schmind* (P). Dalat: Dak Tria, 1400 m**	**15**	**8**
Soulie 1523 (P). "Haut Mekong"	15	12

CHINA

Tibet & Yunnan

Sumatrana Group

Taxus kingstonii

	SR	MC
Soulie 1411 (P). "Tackou et Nekou ("Haut Mekong")	11	12

Wallichiana Group

Taxus florinii

	SR	MC
R.C. Ching 21505 (A). Soc. W. Sikiang: Tamichung	10	–
C. W. Wang 65475 (A). Sikang, Me-kong, Tsa-wa rung, 2500 m	8–9	16
Handel-Mazzetti 2602 (K). Ngaitschekou, 2800–3500 m	11	2
Fleigner et al. 1129 (K). Sahlie Valley on Muzhiyan Shan, 2980 m	10	10

Taxus wallichiana* var. *yunnanensis

	SR	MC
Zhang 916 (PE: **type**). Tibet, Zayul, 2100 m	15	3
Kingdon Ward 6292 (BM). Zayul, 7000–8000 ft	15	3

Sichuan

Sumatrana Group

Taxus celebica

	SR	MC
H. Smith 10401 (BM). Huangnipu, Malingtsang, 1000 m	12	36
Wang 20541 (A). South of Kuan-Hsien, 1160 m	11–12	36
Farges 1895–1897 (P). Tchenkéou Tin	20	32
Farges 128 (P). Tchenkéou Tin	14	24

Taxus kingstonii

	SR	MC
Cheng 1001 (BM). Tachienlu	12	18
Cheng 1475 (P). Tachienlu	12	18

Taxus mairei

	SR	MC
Wilson 1265 (A). Western: Nin Ya-chou Fu, 2000 ft	21	25
Wilson 1265 (US)	15	16
Fang 5811 (P). Nanchuan-Hsien	17	12
Fang 5811 (A). Nanchuan-Hsien	-	16
Hwa 229 (K). *Metasequoia* area	16	12
Fan & Class 91 (A). Kuan-Hsien, Chien-Chang-Shan, 1000 m	16	22
Farges 1436 (P). NE	16	15
Farges 100 (P)	15	16
Law 65 (K). Pei pah	15	8–12
Hwa 27 (A). Li-chuan, Jian-Nan-Hsien, Ta-pen-Ying, 3800 ft	15	27
Smith 10402 (A). W region: between Huangnipu and Yaan (Yachou), Malingtsang, 900 m	14	14
Smith 10402 (S)	15	27
Hwa 27 (A)	14	21
Hwa 27 (K)	14	17

	SR	MC
Legendre 586 (P). Pao Shan NE, 600 m	14	17
Fang 3461 (A). Tienchuan Hsien, Tienchuanchow, 2500–3000 ft	14	20
Fang 3461 (P)	13	17
Fang 12205 (A). Kuan-Hsien, Mt. Tsing-cheng, Chengtu and Kuan-Hsien, 1390 m	14	13
Wang 20600 (A). Wah-Hsien, Mou-tao-chi, Metasequoia area, 1390 m	12–14	16
Hu 1563 (A). Shikong: Tien-Chuan Ling-Kwan, 3000 ft	14–16	–
Farges 128 (P). Tchenkéou Tin	14	17
Farges 128 (P). Tchenkéou Tin	12	24
Fang 3442 (A). Tienchuan-Hsien, Tienchuanchow, 2500–3000 ft	11	12
Fang 3796 (A). UnqLing-Hsien, 5000 ft	12	–
Cao 0152 (BM). Jiabigon, Zhao Quing-sheng, 2500 m	12	10

Wallichiana Group
Taxus chinensis

	SR	MC
Harry Smith 10398 (BM). Tachsiangling, 2600 m	16	6
Peng 502 (Biol. WCUU) (A) Yachow 1600 ft	15	8
d'Legendre (P). 2500 m	14	5
Henry 7155 (US: **type**): E Sichuan: Wushan-Hsien, 2000–3000 m	13	4
Henry 7097 (US)	14	5
Henry 7097 (A)	12	7
Farges 128. NE Sichuan, Tschen-kuu-tin Dist.: (Chenkouting), (P)	13	8
Farges 128 (P)	16	8
Farges 128 (P)	11	7
Wang 1930 (A)	12	4
Wang 22602 (A). Kwang-yun Hsien, 1800 m	12	4

Sichuan (Emei-Hsien: Mt. Emei)

(*T. chinensis*, by increasing number of bare marginal cells)

	SR	MC
Feng 1941 (A)	16–17	4
Fang 16082. (A)	16–17	4
Yu 667 (A). Mt. slope, 2600 m	15	4
Wilson 6200	14–15	4
Lee 3237. (A)	14	4
Hu 8243. (US)	13	4
Hu 8243. (A)	14	5
Lee 4445 (A)	13	4
Yu 669 (A). 1000 m	12	4
Hu 8786. (A)	14	5
Yu 869 (A). 2500 m	12	5
Fang 18420. (A). 2335 m	12–13	6
Lee 4500 (A).	21	7
Ching 1676 (A). Siachu, 2600 ft	16	–
Ching 1676 (P). Siachu, 2600 ft [rectangular cells, papillose midrib in upper half]	16	7
Wang 23656 (A). 2000 m	14	7
Wilson 479 (A).	12	7
Chiao & Fan. 604 (A). 1000 m	10–11	7
Fang 10940 (A). 1200 m	13	7
Fang 15940 (A)	13	8

	SR	MC
Chiao & Fan 464 (A)	10–11	7
Chiao & Fan 464 (P)	12	8
Chiao & Fan 464 (US)	13	9
Hu 8176 (A)	14	9
Wang 20993 (A). W of Wen-chuan Hsien, 2800 m	11	9
Hu 8497 (A)	–	10
Fang 18310 (A)	13	10
Yu 8166 (A). 2400 m	12	10
Fang 15128 (A)	16	11
Fang 15128 (A)	14	11
Wilson 624 (K). S. Wushan, ravine	12	12

Taxus aff. *chinensis*

	SR	MC
Cheng 2890 (A, *Taxus* OCR, in Spjut 2007) W of Lung-an-fu	13–15	8
Cheng 2890 (P)	12	4
Hu 8619 (A). Emei-Hsien, Mt. Emei	12–13	8

Taxus wallichiana

Sichuan: Mt Emei

	SR	MC
Hu 8166 (A)	18	4
Y-s Liu 1196 (A)	15	5
Hu 8542 (A)	15–16	4
Feng 3945 (A)	14	8
Lee 4465 (A)	13	8
Wilson 4053 (A). W Pan-lan-shan W of Kuan Hsien, 5000–6000 ft	14	4

Gansu (Kansu)

Sumatrana Group
Taxus kingstonii

	SR	MC
Meyer 1790 (P)	14	8–12

Ningxia Huizu

Taxus celebica

	SR	MC
Chao 1223 (A). Sikong: Lung Dung An, 1000 m	13	36

Shaanxi (Shensi)

See also *Cuspidata* Alliance, *T. biternata, Purdom s.n.*

Sumatrana Group (T. kingstonii)

	SR	MC
Davis 1872 (P). Tsin-lin au Lao-lin, 3000 m	13	12

Wallichiana Group
Taxus chinensis

	SR	MC
Chens 1893 (P). Central	15	10

Yunnan

Sumatrana Group
Taxus celebica

	SR	MC
Forrest (A)	11	27
Forrest 7798 Gaoligongshan (K)	14	18

Taxus kingstonii

	SR	MC
Forrest 11789 (BM). Shweli-Salween Divide, 10000 ft	13	12
Forrest 11789 (K)	13	7
Forrest 15945 (K). Schweli-Salween Divide	13	16
Forrest 15945 (BM). Schweli-Salween Divide	12	12

	SR	MC
Forrest 9462 (K). Ma-Chang-Kai, valley, 25°30′N, 8000 ft	10	14
Forrest (A). Yunnan, no other data	12	16
Forrest (A). Yunnan, no other data	-	14
Forrest 12087 (S). Schweli-Salween Divide	15	12–14
Forrest 12087 (K)	13–14	14–20
Forrest 9339 (BM)	13	16–18
Rankin 1913 (K). "Yung Chun"	12	14
Rock 7587 (US). Salween E of Tengyueh, to summit of Shweli, Shweli River	12	9

Taxus mairei

	SR	MC
Forrest 15053 (K)	16	12
Maire 131 (BM)	16	15
Maire 1913 (P). Tie'tchang Keol, 700 m	14	28
Maire. (A: **type**). Dongchuan, 700–800 m	13	17

Wallichiana Group

Taxus chinensis

	SR	MC
Feng 630 (A). Ta-hon-shan near Ta-koo, NE of Likiang Snow Range	12	–
Cavalerie 7823 (K)	14	7

Taxus florinii

	SR	MC
Alpine Gard. Soc. Exped. 309 (K). Zhongdian; haba Shan, 3347 m	10	3
Rock 18502 (A). NW: Mt Ludu, NW of Li-Kiang, W of Yangtze	8	4
Rock 18502 (US)	9–10	4
Forrest 19967 (S). NW: Mekong-Salween Divide	8–9	4
Schneider 2918 (A). 3000–3200 m	7	–
Schneider 2918 (K)	9–10	5–6
Schneider 1429 (A). 3500 m	9	13
Schneider 1429 (K)	7	8
Yu 11076 (A). *sine* locality	7–8	9
Yu 7848 (BM); Dokerla, 3100 m	8	7
Rock 11573 (A). Litiping Range, Mekong-Yangtze divide, E of Weihsi	10–11	–
Rock 11573 (A)	9	–
Ching 21980 (A). Litiping, between Likiang and Weihai	10	–
Feng 1809 (A). S Chungtien, Kung- shiang-shu, Snow Mt to Kai-Lou-wei, Yangtze bank 3200 m	8	16
Wang 67735 (A). Wei-si Hsien, 2500 m	10–11	–
Wang 67414. (A). Lung-pan la Champu fung	10–12	5

Taxus aff. *chinensis*

	SR	MC
Feng 11937 (A: type in adnot., *Taxus* OCR in Spjut 2007). Si-chour-Hsien, Faa-doou, 1500 m	16	5
Feng 12105 (A) *l.c.*	14	–
Tsai 59874 (A, *T. phytonii*). Wei-se Hsien 2800 m	12	4
Tsai 58464 (A: type in adnot, *Taxus* SCU in Spjut 2007) Che-tse-lo, 3200 m	14	4
Tsai 58464 (P)	12	6

Taxus wallichiana var. *yunnanensis*

	SR	MC
SB 1981 Exped., Cangshan 0419 (K). W Shangschang, above Yangbi, 2700 m	17	2
Wang 67412 (A). Champu, 2120 m	19	4
1984 SAB Exped 388 (A). Xangbi Xian, W side of Diancang Shan Mt Range, Malultang, Chang Shan, 2700 m, 25°46′ 100°01′	19	6
Handel-Mazzetti 6408 (A). Dji-shan ad boreo-orientem urbis Dali (Talifu), 3200 m	18	4
SB 1981 Exped., Cangshan 0419 (A). W Shangschang, above Yangbi, 2700 m	17	0
SB 1981 Exped., Cangshan 0227 (A). Kiemiu-ingdi above Yangbi, 3000 m	16	4
Wang 72417 (A). Chen-Kang Hsien	15	4
Yu 21036 (A). Salween, Kiukiang Divide, Shawlongwang, 2600 m	14	4

Guizhou (Kweichow)

Sumatrana Group

Taxus mairei

	SR	MC
Steward et al. 328 (A). Ta Ho Yen, Kianakou Hsien, 980 m	14	20
Steward et al. 328 (US)	14	12
Steward et al. 328 (P)	13	18
Cheng 7525 (A: **type,** *T. speciosa* Florin). Kiangkow, 450 m	16	24
Steward et al. 154 (US). Liang Feng Yah, Tsunyi Hsien, 900 m	15–16	19
Steward et al. 154 (A)	12	18
Tsiang 8987 (P). Pichish	14	13
Tsiang 8987 (A). Pichish	11–13	–
SAG Exped. 1981 (GH). Songtao Xian, Lengjiaba, Xiaohe and Dahe Rivers, NE Fanjing Shan mt range, 820–1120 m	12	18

Wallichiana Group

Taxus chinensis

	SR	MC
Cavalerie & Foriupat 2604 (P)	20	7
Cavalerie & Foriupat 2604 (P)	12	5
Cavalerie & Foriupat 2604 (P)	11	5
SAG Exped. 1981 (US).	12	6
SAGB 1986 Exped. 1854 (A). Yinjiang Xian, Xiapingsho, W Fanjing Shan range, 1 100–1400 m	16–17	10
SAGB Exped.1046 (A). Jiangkou Xian, Daiyenpeng, Kaitu River, SW Fanjing Shan range, 750–1000 m	12	12

Hubei (Hupeh)

Wallichiana Group

Taxus chinensis

	SR	MC
Chow 76099 (A). Shenlungkai	15	7
SA 1980 Exped. 1540 (A). S of Jiuhuping Forest along Jizigou canyon, 1900 m	13	6
Wilson 1265b (A). Western: Nin Ya-chou Fu, 2000 ft	13	4

	SR	MC
SA 1980 Exped. 777 (A).Western: Shennongjia For. Dist., NE Guanmenshan, S of Shicao river, 1150 m	13	7
SAB 1980 Exped. 1824 (GH). Shibapan, 1850 m	13	7
SAB 1980 Exped. 1824 (A)	12	6
Wilson 716 (A)	12	7

Taxus aff *chinensis* (*Taxus* sp. SCU in Spjut 2007)

	SR	MC
SA 1980 Exped. 585 (A). Western: Shennongjia For. Dist. 331°30'N 110°30'E, 1200–1400 m	13	8

Sumatrana Group

Taxus mairei

	SR	MC
Gressitt 2507 (A). *Metasequoia* Area, between Ta-yin-pin & Chunglo, Shui-sa-pa, 900 m	12	14

Anhui (Anhwei)

Sumatrana Group

Taxus mairei

	SR	MC
Ching 3168 (A). Southern, Chanen, 300 ft	12–13	12

Wallichiana Group

Taxus chinensis

	SR	MC
R-C Ching 2622 (A). S Anhui, Clas Hara Shan	17	5
R-C Ching 2622 (US)	13	4
Cheng 4026 (BM). Wangshan	11	6

Henan (Hunan)

Taxus mairei

	SR	MC
Fan & Li 644 (A). Ma-Ling-Tung, Sinning Hsien, 600 m	15	18
Fan & Li 296 (A). Changning Hsien, Yang-Shan, 680 m	15	–
Fan & Li 296 (BM)	14	12

Jiangsu (Kiangsu, Kiangshi)

Taxus mairei

	SR	MC
Wang-Te-Hui 445 (A). Ningdu, Yuntungtschi	9–12	25
Y.K. Hsiung 6443 (A). NW, Si-ho, Hwang-kong-shan Mt	-	11
Wang-Te-Hui 458 (A). Lienhwa-shan, 800 m	-	10–12
Chow 80325 (BM). Nanking, 75 m	12	16

Guangxi (Kwangsi)

Sumatrana Group

Taxus celebica

	SR	MC
Ching 5976 (US). Bin Long, Miu Shan, N Luchen, border of Kweichow, 4000 ft	15–16	32
Ching 5976 (A)	14–15	31

Taxus mairei

	SR	MC
Chiao 18795 (US). Lu Shan	16	6–10

Wallichiana Group

Taxus chinensis

	SR	MC
Steward & Cheo 947 (P). 2110 m	15	4
Steward & Cheo 947 (BM). San Chiang Hsien, 2110 m	12	4

Zhejiang (Chekiang)

Taxus mairei

	SR	MC
Cheng 3617 (US). Eastern: Tien-Mu-Shang	14–16	10
Keng 317 (A). Taishun-Hsien	13	18
Hu 342 (A). Tien-Tai-Shan, 1300 m	13	15
S. Chen 1063 (A)	12	18
(US: 145110). Tien Tai Shan	12	–
Ching 2489 (A). S: King Yuan, 300–800 m	11	20
Ching 2489 (US)	13	14

Taxus sumatrana

	SR	MC
Hu 1628 (A). Lin-an Hsien, 1200 ft	14	16
Hu 550 (A). Y-Chien Hsien, 1000 ft	12	15

Guangdong

Taxus celebica

	SR	MC
Nanling Exped. 1838 (A). Ruyuan Xian	-	31

Taxus mairei

	SR	MC
Tsang 20694 (US). Loh Ch'ang Dist., Chong Uen Shan near Kau Fung	13–15	14
Tsang 20694 (A)	-	24
Chiao 14510 (A). Tien-Tai-Shan, 1300 m	12	24
Chiao 14510 (US)	12	14
Tsiang Ying 1425 (A). Hung-mio to Mio- lan, Jui-feng, Lokohong Hsien N.R. Region, 1340 m	12	14
Tsiang Ying 1425 (A, different label)	14	24
Tsiang Ying 1425 (P, specimen does not appear to be the same plant as in A)	13	5–7

Fujian (Fukien)

Sumatrana Group

Taxus mairei

	SR	MC
Price 1258b (K). Ing-dan E. Fookma	12	26
Sheng 1544 (K). Naping, 800 m	16	14
Chung 2865 (A). Yeuping, Shih-Sun-Keng, 650 m	13	14
Chung 2865 (K)	12	16
David (P). W: Mts	12	18
Chung 3581 (A). Buong Kang, mt slope, 700 m	9	24
He-Guosheng 1544 (US). Naping, 800 m	16	6

Wallichiana Group

Taxus aff *chinensis*

	SR	MC
H.H. Chung 3866 (A). Puchen	11	5

Taiwan

Sumatrana Group

Taxus kingstonii

	SR	MC
Hsu 1651 (PH). Mt. Pasein-san, Taichang Hsien	16	8
Liu 389 (PH). Mt. Ammashan, Taichung Hsien	15	8
Liu 389 (A)	14	–
Hsu (PH). Mt. Pasan-shan, Taichang Hsien	14	9
Wilson 9738 (BM, **isotype**). Arisan Prov.: Kagi, 2833 m	13	9
Wilson 9738 (A: **holotype**)	10–11	8
Liu 437 (US). Taiklang, Shih-wan-hsi, Pa-Hsien-shan, 2250 m	12	9

	SR	MC
Nakahara (PH). Arizan Prov.	11	9
C-j Chang, Tongshi 6 (wba)		
27 Sep 93	14	9
26 Nov 93	13	7
06 Dec 93	12	9
09 Dec 93	13	9
27 Jan 94.	13	8
13 Jan 94 (new growth)	13	8
13 Jan 94 (old growth)	11	9

Taxus mairei

	SR	MC
C-j Chang 1–2,4–5, 7–10 (wba). Hua-lien		
1 16 May 94	12	18
1 03 Aug 94	12	18
2 16 May 94	11–12	27
2 03 Aug 94	11–12	20
4 16 May 94	12	21
4 03 Aug 94	12	17
5 16 May 94	10–11	23
5 03 Aug 94	12	24
9 16 May 94	15	19
9 03 Aug 94	12	24
10 16 May 94	12	14
10 03 Aug 94	11	18
7 16 May 94	14	8
7 03 Aug 94	14/15	6
8 16 May 94	16	9
8 03 Aug 94	16	8

Taxus sumatrana

	SR	MC
de Laubenfels P 671 (A). Tai-shu Shan For. Dist., 2000 m (Rt. 210, 7km)	10–11	6
de Laubenfels P 670 (A). l.c.	10	8
C-j Chang		
3 (wba) 16 May 94	11	13
3 03 Aug 94	10–11	12

Wallichiana Group
Chinensis Subgroup

	SR	MC
Wilson 11154D (A: **type** in adnot.). Karenko Prov.: mts W of Karenko	12–13	6
C-j Chang, Tongshi 5 (wba)		
27 Sep 93	14	4
26 Nov 93	12	5
06 Dec 93	11	5
09 Dec 93	12	5
13 Jan 94	11	4
C-j Chang, Tongshi 7 (wba).		
27 Sep 93	14	7
26 Nov 93	14	9
06 Dec 93	14	5
09 Dec 93	14	5
27 Jan 94	14	5
C-j Chang 6 (wba). Hua-lien		
16 May 94	09–10	8
03 Aug 94	11	8–9

	SR	MC
Origin?		
Y. Sugilara, Ex TUS (GH).[arbitrarily placed here]	13	3
THE PHILIPPINES		

Sumatrana Group
Taxus sumatrana

	SR	MC
Merrill 4595 (US). Lepanto Dist., Mt. Data	12–13	14
de Laubenfels P650 (GH). Benguet, 58 km N of Baguio, 2100 m	11–13	13
Whitehead 1896 (BM). NW central Luzon: 5000–7000 ft	12	12
Williams 1002 (US). Benguet: Mt. St. Tomas	12–13	10–12
Leano 20672 (US). Benquet Prov. Mt. St. Tomas	11–13	9
Vidal 623 (GH); Mt. Banahao, Pr. Tayabas	11	7

Wallichiana Group
Chinensis Subgroup

	SR	MC
E.C. Leano 25128 (US). Luzon: Benquet Prov., Mt. St. Tomas	16	4
Elmer 6244 (P). Mt. St. Tomas	14	4
Elmer 6244 (US)	12	4
Loher 4850 (K). Luzon: central.	14	4
Loher 4850 (US)	12	4
Curran 5015 (P). Benquet Prov., Mt. Tonglan	14	7
Curran 5015 (PH)	14	4
Jacobs 7171 (K). Luzon: Mt. Pulog, 2200–2300 m	14	2–3
Ramos & Edaño 40234 (K). Luzon: Lepanto, Mt. Data	14	2
Ramos & Edaño 40234 (P)	12	4
Wilkes Exped. 1838–1842 (GH). Luconia: Mt. Mahaihai	13	2
Curran 7911 (US). Luzon: Benquet Prov., Mt. Banajao	12/13	5
Merrill 839 (US). Luzon, Benquet Prov.	12	3–4
Merrill 839 (US)	12	4
Ocampo 27920 (A). Mt. Banajao	11	–
Ocampo 27920 (P)	11	–
de Laubenfels P669 (GH). Luzon: Laguna Prov., Mt. Banajao, 2100 m	11	4
de Laubenfels P668. (GH: **type** in adnot.)	-	4
Herb. Hook. (K). Luconia, 7600 ft	10–11	4
Loher 7139 (US)	-	3
Sulit 2350 (A). Luzon: Benguet Prov., Mt. Pauai, 2450 m	15	8
Alvarey 18369 (BM). Benquet Prov.	12–14	8
INDONESIA		
Sulawesi (Celebes)		

Sumatrana Group
Taxus celebica

	SR	MC
Everett 35 (K: **type,** *Podocarpus celebicus* Hemsley). Bonthian Peak, 7000–10,000 ft	14–15	22

Taxus sumatrana

	SR	MC
Teysmann 14190 (U). Bonthian	11–13	16

	SR	MC
Wallichiana Group, Chinensis Subgroup		
Neth. Ind. For. Serv. bb:19577 (A). Ond. Malili 1800 m	12–15	12
Neth. Ind. For. Serv. bb:20887 (K). Goua Lambaja, 2000 m	11	4

Sumatera

	SR	MC
Sumatrana Group		
Taxus sumatrana		
Teysmann s.n. (U: **type**). Sumatra: western, Fort de Kock, 3000 m	12–14	12
de Voogd 1503 (K). Palembang, Dempo, 1000 m	13	10
Wallichiana Group, Chinensis Subgroup		
Boschprochation 7709 (U). Tharolanden, 1400 m	14	4

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